Greenness indices from digital cameras predict the timing and seasonal dynamics of canopy-scale photosynthesis

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2 Greenness indices from digital cameras predict the timing and seasonal dynamics of canopy-

3 scale photosynthesis

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41

42

43 **ABSTRACT**

44 The proliferation of digital cameras co-located with eddy covariance instrumentation provides

45 new opportunities to better understand the relationship between canopy phenology and the

46 seasonality of canopy photosynthesis. In this paper we analyze the abilities and limitations of

47 canopy color metrics measured by digital repeat photography to track seasonal canopy

48 development and photosynthesis, determine phenological transition dates, and estimate intra-

49 annual and interannual variability in canopy photosynthesis. We used 59 site-years of camera

50 imagery and net ecosystem exchange measurements from 17 towers spanning three plant

51 functional types (deciduous broadleaf forest, evergreen needleleaf forest and grassland/crops) to

52 derive color indices and estimate gross primary productivity (GPP). GPP was strongly correlated

53 with greenness derived from camera imagery in all three plant functional types. Specifically, the

54 beginning of the photosynthetic period in deciduous broadleaf forest and grassland/crops and the

55 end of the photosynthetic period in grassland/crops were both correlated with changes in

56 greenness; changes in redness were correlated with the end of the photosynthetic period in

57 deciduous broadleaf forest. However, it was not possible to accurately identify the beginning or

58 ending of the photosynthetic period using camera greenness in evergreen needleleaf forest. At

59 deciduous broadleaf sites, anomalies in integrated greenness and total GPP were significantly

60 correlated up to 60 days after the mean onset date for the start of spring. More generally, results

61 from this work demonstrate that digital repeat photography can be used to quantify both the

62 duration of the photosynthetically active period as well as total GPP in deciduous broadleaf

63 forest and grassland/crops, but that new and different approaches are required before comparable

64 results can be achieved in evergreen needleleaf forest.

65

1

INTRODUCTION

Climate change impacts on vegetation phenology have been widely documented across a range of biomes and plant functional types (Richardson et al. 2013). In particular, long-term records of leaf and flower phenology in temperate and boreal forest indicate that spring onset is occurring earlier (Miller-Rushing and Primack 2008, Thompson and Clark 2008, Aono and Kazui 2009, Linkosalo et al. 2009), and more generally, that growing seasons are becoming longer on decadal to millennial scales (Menzel 2000). Studies using satellite remote sensing have documented trends towards longer growing seasons over large regions of in mid- and high-latitude ecosystems of the Northern Hemisphere (Myneni et al. 1997, Zhang et al. 2007, Jeong et al. 2011, Xu et al. 2013). At lower latitudes, warmer temperatures have led to earlier spring phenology and longer growing seasons in Mediterranean ecosystems (Penuelas et al. 2002, Gordo and Sanz, 2010), while desert plant communities have experienced shifts in species composition in response to changes in the timing of winter precipitation (Kimball et al. 2010).

While a large number of studies have identified widespread patterns of change, the impacts of changes in phenology on ecosystem function and feedbacks to the climate system remain poorly understood and quantified (Richardson et al. 2013). For example, multi-site comparisons show that growing season length is positively correlated with net ecosystem productivity (NEP; Churkina et al. 2005, Baldocchi 2008), but spatial patterns observed across sites are not identical to temporal patterns at individual sites, which are driven primarily by interannual variability in weather (Richardson et al. 2010). Warmer springs and longer growing seasons have been shown to increase annual carbon uptake in boreal deciduous forest (Barr et al. 2004, 2007), mixed temperate forest (Dragoni et al. 2011) and evergreen needleleaf forest (Richardson et al. 2009a,

91 2010). In subalpine forest, on the other hand, longer growing seasons can lead to lower NEP if

92 warmer temperatures (Sacks et al. 2007) or shallower spring snowpacks (Hu et al. 2010) reduce

93 soil moisture sufficiently to create drought conditions. Similarly, drought conditions in grassland

94 can also shorten the growing season length, thereby lowering annual NEP (Flanagan and

95 Adkinson 2011).

96

97 Because phenology is a key regulator of ecosystem function, substantial effort has recently been

98 devoted to expanding networks that track seasonal vegetation dynamics (Morisette et al., 2009).

99 Methods to monitor phenology fall into two broad categories: visual observations and remote

100 sensing. Visual observations provide the oldest and longest running phenology records in

101 existence (e.g., Aono and Kazui 2008), but visual observations are labor intensive to collect, and

102 the spatial extent of observations collected by an individual is inherently limited. Spaceborne

103 remote sensing, which provides synoptic and global views of land surface phenology and its

104 responses to natural climatic variability, helps to address this limitation (Piao et al. 2006,

105 Dragoni and Rahman 2012, Elmore et al. 2012). However, imagery from remote sensing

106 platforms such as the Moderate Resolution Imaging Spectradiometer (MODIS) is often collected

107 at coarse spatial resolutions (250-500m) that encompass considerable landscape heterogeneity

108 within each pixel. An additional weakness is the relatively low temporal resolution of some

109 space-borne remote sensing instruments. While coarse spatial resolution sensors such as MODIS

110 provide observations with repeat intervals of 1-2 days, moderate spatial resolution sensors such

111 as Landsat provide a revisit frequency of 16 days, a relatively long interval for capturing rapid

112 changes during seasonal transition periods. In both cases, persistent cloud cover can significantly

113 reduce the frequency of useable observations, which can substantially decrease the utility of

114   space-borne remote sensing for observing and characterizing the timing of key phenological

115   transitions.

116

117   Digital repeat photography, a form of near-surface remote sensing, provides data at higher

118   temporal frequency and finer spatial scale than satellite remote sensing (Richardson et al.

119   2009b). Specifically, digital repeat photography can provide imagery that is nearly continuous in

120   time, rarely obscured by clouds, and robust to variation in illumination conditions (Sonnentag et

121   al. 2012). Exploiting this, color indices derived from digital repeat photography have been used

122   to characterize the phenology of diverse plant communities and functional types (PFT) including

123   deciduous broadleaf forest (Richardson et al. 2007, Ahrends et al. 2008, Ide and Oguma 2010,

124   Sonnentag et al. 2012, Hufkens et al. 2012, Dragoni et al. 2011), evergreen broadleaf forest

125   (Zhao et al. 2012), evergreen needleleaf forest (Richardson et al. 2009b, Ide and Oguma 2010,

126   Bater et al. 2011), desert shrublands (Kurc and Benton 2010), bryophyte communities (Graham

127   et al. 2006) and invasive plants (Sonnentag et al. 2011). Several studies have used these data to

128   evaluate uncertainties in satellite-based phenological monitoring (Graham et al. 2010, Hufkens et

129   al. 2012, Elmore et al. 2012, Klosterman et al. 2014).

130

131   Color indices derived from digital repeat photography have also been correlated with canopy

132   photosynthesis in deciduous broadleaf forest (Richardson et al. 2007, 2009a, Ahrends et al. 2009,

133   Mizunuma et al. 2012), grasslands (Migliavacca et al. 2012), and desert shrublands (Kurc and

134   Benton 2010). However, each of these studies was limited to one or two sites and it is unclear

135   how well results from these efforts generalize within and across PFTs at regional to continental

136   scales. Further, a large proportion of previous studies have focused on temperate deciduous

137   forest. Not only does the relationship between annual carbon exchange and the length of the

138   carbon uptake period vary substantially across PTFs (e.g., Richardson et al. 2010), but

139   relationships among camera-based color metrics, phenology, and carbon exchange remain under-

140   studied in ecosystems and PFTs outside of deciduous broadleaf forest (Richardson et al. 2013).

141   Hence, there is a need for improved understanding regarding how canopy photosynthesis is

142   linked to canopy phenology across and within PFTs, and by extension, the role of digital repeat

143   photography for studying these relationships.

144

145   With these issues in mind, our objective in this study was to perform a systematic analysis of

146   digital repeat photography as a tool for understanding the relationship between canopy

147   phenology and canopy photosynthesis, both within and among multiple PFTs. To this end, the

148   specific questions guiding this study were:

149

150   1) Can camera-derived color indices be used to monitor the seasonality of GPP within and across

151   multiple PFTs?

152   2) How does the relationship between canopy phenology and GPP vary within and across PFTs?

153   3) What is the relationship between dynamics in greenness measured from digital camera

154   imagery and key phenophase transitions in different PFTs?

155   4) Can interannual variation in annual GPP be estimated using camera-derived color indices?

156

157   To address these questions, we used data from the PhenoCam network of co-located cameras and

158   eddy covariance towers to assess the relationship between canopy phenology and the seasonality

159   of photosynthesis. Our study, conducted across a range of PFTs, provides the most

160 comprehensive analysis of canopy development and photosynthesis using digital repeat

161 photography to date, and provides useful new understanding regarding the ability of camera-

162 derived color indices to track the seasonality of GPP across space and time.

163

164 **METHODS**

165 **Study Sites**

166 The study spanned 13 geographically distinct research sites, including 17 flux towers in total

167 (Table 1; Appendix A). We used all possible sites that were members of both the PhenoCam

168 (http://phenocam.sr.unh.edu/) and the AmeriFlux (http://ameriflux.ornl.gov/) or Canadian

169 Carbon Program (http://fluxnet.ornl.gov/site_list/Network/3) networks. In addition, we included

170 four towers, managed by the University of Illinois (UI), that were not members of either

171 network. Each site was dominated by one of three PFTs: deciduous broadleaf forest (DBF),

172 evergreen needleleaf forest (ENF), and grassland/crops (GRS; Table 1). The Groundhog site in

173 Ontario is most accurately described as mixed ENF/DBF; here, we group it with ENF sites

174 because conifer species are dominant. Together, measurements from these sites comprised 59

175 site-years of concurrent flux and camera data, with 26, 11, and 22 site-years in DBF, ENF and

176 GRS PFTs, respectively. Most sites had 2-5 years of data. One notable exception, however, is the

177 ARM site in Oklahoma, where data were collected nearly continuously from 2003-2011. One of

178 the UI sites featured a crop rotation from maize to soybean in the second year (out of two),

179 which caused significant changes in the magnitude of carbon fluxes. To address this, we treat the

180 two site-years (2009 vs. 2010) as separate sites: UI Maize and UI Soy.

181

182 **Digital repeat photography**

183   On each eddy covariance tower, the digital camera was installed in a fixed position, with a view

184   across the top of the canopy. Cameras were pointed north to minimize shadows and lens flare,

185   enclosed in commercial waterproof housings, and inclined up to 20° below horizontal. Most

186   cameras collected photos, which were saved in 24-bit JPEG format, at 30-60 minute intervals,

187   12-24 hours a day. Exceptions include Bartlett (10-20 minute intervals, 12:00-14:00) and ARM

188   Oklahoma (1 midday photo). Half of the towers used StarDot NetCam XL or SC cameras

189   (StarDot Technologies, Buena Park, CA), while the other sites used cameras from a variety of

190   manufacturers (Table 1). To minimize the impact of variation in scene illumination (e.g. clouds

191   and aerosols), auto white/color balance was turned off, and exposure adjustment for each camera

192   was set to automatic mode. Note, however, that Vaira was an exception in this regard. To correct

193   for variability induced by auto color balancing at this site, we used a grey reference panel in the

194   camera field of view (e.g., Jacobs et al. 2009).

195

196   Images were either archived by the site investigator or automatically transferred to the

197   PhenoCam server *via* file transfer protocol (FTP). Time series were first visually inspected for

198   camera shifts and changes in field of view. Noting these changes, we processed the image

199   archives to extract regions of interest (ROI) that encompassed all portions of the full canopy

200   within the foreground (Fig. 1). At Vaira, the ROI was restricted to the grass portion of the image,

201   excluding distant oak trees from analysis. To quantify canopy greenness, we calculated the green

202   chromatic coordinate (GCC), which is widely used to monitor canopy development and identify

203   phenological phase changes (Richardson et al. 2007, Ahrends et al. 2009, Sonnentag et al. 2012,

204   Zhao et al. 2012):

205
$$GCC = \frac{DN_G}{DN_R + DN_G + DN_B}$$
(1)

206   where *DN* is the digital number and *R*, *G* and *B* denote the red, green and blue channels,

207   respectively. For completeness, we also calculated the Excess Green (ExG) index:

208    $$ExG = 2DN_G - (DN_R + DN_B) \tag{2}$$

209   which has been shown to be less noisy than GCC in some coniferous canopies (Sonnentag et al.

210   2012). To characterize canopy coloration in fall, the red chromatic coordinate (RCC) was

211   calculated using the same form as Eq. 1, substituting DN_R in the numerator.

212

213   Following Sonnentag et al. (2012), we calculated the 90th percentile of GCC, ExG and RCC

214   values for 3-day moving windows, yielding up to 122 observations each year. Only photos taken

215   during daylight hours (6:00 – 18:00 local time) were included, and any images with under-

216   exposed ROIs (which we defined as <15% color saturation, or DN < 39, in any band) were

217   excluded. We did not exclude photos due to poor weather conditions or snow, as the 90th

218   percentile filter successfully removed these (Sonnentag et al. 2012). To eliminate any residual

219   noise we removed GCC or ExG values that exceeded ±2 standard deviations of the mean within

220   27-day windows. To account for changes in camera settings or shifts in camera fields of view,

221   GCC, RCC and ExG values were manually screened and rescaled (as needed) to preserve a

222   smooth and continuous time series at each site.

223

224   We used nonlinear least squares regression to fit logistic functions to GCC, RCC and ExG time

225   series, which were then used to estimate phenophase transition dates from DBF and GRS sites

226   (*e.g.,* Fisher et al. 2007, Richardson et al. 2009b). For GRS sites, we used separate logistic

227   functions in spring and fall:

228    $$GCC(t) = a_s + \frac{b_s}{1+e^{(c_s - d_s t)}} \tag{3a}$$

229
$$GCC(t) = a_f + \frac{b_f}{1+e^{(c_f+d_f t)}}$$
(3b)

230   where t is the day-of-year and the remaining terms are empirically estimated coefficients. For

231   DBF sites, we used the modified logistic function presented by Elmore et al. (2012), which

232   includes an additional parameter (a_2) that accounts for "summer greendown" that is widely

233   observed in DBF greenness time series (Keenan et al., 2014):

234
$$GCC(t) = a_1 + (b - a_2 \times t)(\frac{1}{1+e^{(c_s-d_s t)}} - \frac{1}{1+e^{(c_f-d_f t)}})$$
(4)

235   Note that in Equation 4, a_1+b denotes the early summer maximum GCC, while the minimum

236   summer GCC value preceding fall coloring is given by ($b - a_2*t$). Coefficients in Equations 3

237   and 4 were estimated using the Levenberg-Marquardt method.

238

239   Following a widely used remote sensing approach (e.g., Zhang et al. 2003), phenophase

240   transitions were determined by calculating local minima and maxima in the curvature change

241   rate of Equations 3 and 4. In spring, maxima correspond to dates of leaf unfolding (start of

242   spring) and maximum greenness (end of spring). In autumn, the onset of fall coloring (start of

243   senescence) and leaf abscission (end of fall) correspond to the timing of minima. The midpoints

244   of each season, middle of spring and middle of fall, were identified using the local minimum and

245   maximum, respectively. We also tested one additional method to estimate the end of fall in DBF

246   sites based on the timing of maximum fall coloring (Richardson et al. 2009b), which was

247   determined using the date of the maximum RCC value in the second half of the growing season.

248

249   Early analysis indicated that the logistic function provided a poor representation of GCC

250   dynamics at many ENF sites; a separate method was needed to explore links between GCC and

251   GPP seasonality in evergreen sites. Hence, we calculated splines along GCC curves and

252 examined correlations between dates at which a range of GCC thresholds (5–75% of seasonal

253 amplitude, in 5% intervals) were reached, and dates at which a similar range of GPP thresholds were

254 reached.

255

256 **Eddy covariance data**

257 To assess the ability of camera-based indices to capture seasonal dynamics in carbon fluxes, we

258 compared color indices with estimates of GPP derived from eddy covariance measurements.

259 To do this we used 30-minute non-gap-filled NEE data to estimate GPP, except at the Harvard

260 Forest and Morgan Monroe sites, where only hourly data were available. NEE was partitioned

261 into GPP (μmol CO_2 m^{-2} s^{-1}) using the Q_{10} method (Raich and Schlesinger 1994):

262 $$GPP = NEE - Reco = NEE - Rref \times Q_{10}^{(T-Tref)/10} \qquad (5)$$

263 where R_{ref} is a scaling parameter, Q_{10} is the temperature sensitivity of ecosystem respiration

264 (R_{eco}), and T_{ref} (= 10°) is the base temperature where $R_{eco} = R_{ref}$. Friction velocity (u_*) filtering

265 was used to remove nocturnal NEE measurements when there was insufficient turbulence using

266 site-specific u_* values. The Q_{10} function was estimated independently for every site-year,

267 yielding 30-minute estimates of R_{eco} and GPP. When available, we compared our GPP estimates

268 with estimates provided by site investigators. Results from this comparison showed that the

269 estimates were in close agreement (mean R^2 = 0.95; range: 0.91-0.98).

270

271 To make the GPP data comparable to the camera-based color indices, we calculated the mean

272 daily-integrated GPP (g C m^{-2} d^{-1}) across the three-day periods over which the camera data were

273 processed. In addition, we also calculated mean daytime instantaneous flux rates (calculated

274 across all daytime hours, defined as PPFD $\geq$ 5 μmol m^{-2} s^{-1}), as well as estimates of the light-

275   saturated rate of photosynthesis (A_{max}, μmol CO_2 m^{-2} d^{-1}), which was derived by fitting a

276   Michaelis-Menten light response function to the high-frequency (hourly or half-hourly) flux

277   measurements. The use of these alternative metrics did not change our interpretation of the

278   results described below. To allow comparison at annual time scales, we calculated annual GPP

279   sums, using the same Q_{10} method as above, but including gap-filled NEE. When gap-filled NEE

280   data were not provided by site investigators, we used an online tool (http://www.bgc-

281   jena.mpg.de/~MDIwork/eddyproc/) that implements standardized gap filling methods

282   (Reichstein et al. 2005).

283

284   To evaluate GCC as a predictor of photosynthesis, daily GPP was regressed against 3-day GCC

285   for each tower site. We also regressed the mean daytime instantaneous flux rate (GPP$_{30}$;

286   averaged over equivalent 3-day periods) against GCC, which allowed us to assess this

287   relationship independent of day length. Goodness-of-fit was based on the coefficient of

288   determination (R^2), calculated using linear and quadratic functions at a significance level of 0.05.

289

290   A key goal of this analysis was to assess how well dynamics in GCC capture changes in

291   photosynthetic activity corresponding to phenological transitions. For example, one question we

292   examined was, "Does start of spring, estimated by GCC, correspond to the first day of

293   photosynthesis (GPP > 0 g C m^{-2} d^{-1}) in spring?" To compare relative photosynthetic capacity

294   across sites, we fit smoothing splines to the daily GPP time series for each of the six DBF sites

295   and calculated the percentage of maximum annual flux (maximum daily GPP within a given year

296   = 100%) at 1% intervals along the estimated splines. These data were then pooled, providing a

297   composite DBF data set of 19 site-years. Using phenophase transition dates (start of spring,

298 middle of spring, middle of fall, end of fall) extracted from the GCC and RCC time series, we

299 performed geometric mean regression between camera-derived dates and a range of flux

300 amplitudes (1-90%). Goodness-of-fit was evaluated using the coefficient of determination and

301 the slope of the regression. Bias was quantified using the mean deviation, and accuracy was

302 evaluated using the root mean square deviation (RMSD) between transition dates estimated from

303 GCC data and transition dates estimated from GPP data.

304

305 To explore these relationships at the GRS sites, we pooled data from the four UI sites and

306 performed a parallel analysis. The ARM site in Oklahoma was excluded because both the flux

307 data and the camera data included mixtures of differing phenological patterns associated with

308 multiple crop cycles. We also excluded the Vaira site because it is characterized by

309 asynchronous seasonality (winter active vs. summer active elsewhere) relative to the rest of the

310 sites in our analysis of transition dates. To compare the timing of maximum greenness ($GCC_{90\%}$)

311 and carbon flux ($GPP_{90\%}$), we determined the dates when each metric reached 90% of the

312 maximum annual value at each site using only complete site-years.

313

314 Because the rates of spring increase and fall decrease in daily GPP or GCC can vary between

315 years (see Richardson et al. 2010), dates corresponding to the start and end of the growing season

316 may not fully characterize patterns of interannual variability in phenology. To assess this, we

317 tested the hypothesis that during the spring or fall transition periods time-integrated GCC values

318 provide more information about anomalies in GPP than start-of-season or end-of-season dates

319 estimated from GCC time series. To do this, we first re-scaled the GCC and GPP data to account

320 for differences across sites in the magnitude of carbon fluxes and canopy greenness. This

321   provided normalized time series of daily GPP and GCC, both on a scale from 0 to 1. We then fit

322   splines to the normalized GPP and GCC values over 60 day-periods following the earliest start of

323   spring and preceding the latest end of fall, and calculated the integral under each spline curve

324   using numerical approximation. These integrals were then converted to anomalies relative to

325   each site-level mean and used to calculate linear correlations between integrated GCC anomalies

326   and integrated GPP anomalies. To determine whether integrated GCC values provide greater

327   explanatory power than discrete dates such as the start of spring, we compared these results with

328   linear correlations between phenophase transition date anomalies and integrated GPP anomalies.

329   Lastly, we tested whether spring and fall greenness anomalies were correlated with integrated

330   annual GPP anomalies via multiple linear regression, using spring and fall normalized integrated

331   GCC anomalies as independent variables and annual GPP anomalies as the response variable.

332

333   **RESULTS**

334   **Canopy development and photosynthesis – patterns among plant functional types**

335   Time series of GCC and daily GPP (Fig. 2; Appendix B) demonstrate broadly consistent

336   relationships within each of the three PFTs, with some notable exceptions. DBF and GRS sites

337   exhibited clear seasonality in both GCC and GPP, with high values during the photosynthetically

338   active season and low values during the inactive season. GRS sites exhibited shorter but well-

339   defined growing seasons compared to those in DBF (Fig. 2c). In ENF sites, the annual cycle in

340   GCC was roughly sinusoidal, with a relatively short period of minimum values in winter (Fig.

341   2b). Relationships between GCC and GPP in both the active and dormant seasons were phase-

342   shifted, with spring increases in GCC preceding those in GPP, and autumn decreases in GCC

343   lagging behind GPP.

344

345   We also noted distinct differences among the PFTs with regard to the amplitude and range of

346   GCC values. In DBF and GRS, GCC time series were characterized by low values (0.33-0.36)

347   during the winter and high values (0.40 to 0.50) in peak growing season (Table 1; Appendix B).

348   In contrast, the dynamic range of ENF was much smaller (e.g., seasonal amplitude was 0.04

349   GCC units for Chibougamau vs. 0.08 GCC units for Harvard, Figs. 2b and 2a, respectively). The

350   smallest range was observed for Wind River, where GCC values varied by just 0.03 throughout

351   the year. There was also a wide range in GPP among PFTs owing to differences in ecosystem

352   productivity arising from factors such as species composition, leaf area, and local climate.

353   Across all sites and PFTs, daily GPP values showed strong seasonal patterns, but there was

354   substantial day-to-day variation caused by changes in short term environmental conditions (e.g.

355   clouds, vapor pressure deficits, and soil moisture) that limit short-term productivity, and by

356   extension, decrease correlation between GPP and GCC on short (i.e., hours to days) time scales.

357

358   **Canopy development and photosynthesis – patterns within plant functional types**

359   DBF sites exhibited two primary modes of variation in GCC during the photosynthetically active

360   season. First, over the course of two or three weeks in late spring, GCC tended to exhibit a

361   distinct late-spring "green peak" that was not observed in either ENF or GRS. Second, following

362   this peak, GCC tended to gradually decline over roughly three months, leading to a decrease in

363   GCC of about 30% relative to the seasonal amplitude. At the onset of leaf coloration, GCC

364   tended to decrease rapidly, leading into the annual winter minimum. Daily GPP, by contrast,

365   increased more slowly throughout the spring, reaching its maximum value 2-4 weeks after the

366 GCC peak. And, whereas GCC remained high during the summer months, daily GPP tended to

367 decline almost immediately after its peak, well in advance of the fall decline in GCC.

368

369 As we noted above, daily GPP exhibited substantial day-to-day variability in all PFTs. At the

370 Missouri Ozarks site in 2007, however, daily GPP decreased sharply in July, nearly two months

371 before the autumn decrease in GCC, likely in response to moisture stress (Yang et al. 2010).

372 Otherwise, covariance between daily GPP and GCC for DBF sites was generally strong overall

373 ($R^2 = 0.50 - 0.79$; Table 2; Fig. 3a; Appendix C) and tended to be linear at lower values of GCC.

374 At higher values of GCC, however, there was little or no relationship between daily GPP and

375 GCC for most DBF sites, which reflects the fact that daily GPP during mid-summer is controlled

376 by day-to-day variation in weather that does not affect canopy greenness on short time scales.

377 Correlations between daily GPP and GCC were comparable with those between GCC and GPP_{30}

378 (Table 2), indicating that GCC-GPP relationships are robust and independent of seasonal

379 changes in day length.

380

381 ENF sites were characterized by unique patterns of seasonality in GCC and GPP. Most notably,

382 the period associated with minimum GCC values during winter dormancy was short lived. At

383 most ENF sites GCC continued to decline into early winter, even when daily GPP was near zero,

384 before rising again in late winter well in advance of the spring onset of photosynthesis. This

385 pattern was not observed at the Wind River site, which was photosynthetically active throughout

386 almost the whole year (Appendix B). Among all ENF sites, the summertime peak in GCC

387 occurred close to the peak in daily GPP. Overall, correlations between daily GPP and GCC were

388 almost as strong ($R^2 = 0.53 - 0.76$; Appendix C; Table 2) as those for DBF sites. As with DBF,

16

389　　correlation between GCC and GPP_{30} were comparable with those between GCC and daily GPP

390　　(Table 2).

391

392　　For all but one GRS site, correlations between daily GPP and GCC were high (R^2 = 0.80-0.90;

393　　Table 2; Appendix C), and the relationship was linear. Similar to the ENF sites, GCC at GRS

394　　sites exhibited a short summer plateau. At the UI Switchgrass and UI Prairie sites, GCC was

395　　modestly phase shifted, with GCC leading daily GPP in spring and lagging daily GPP in fall.

396　　Covariance between GPP and GCC at the ARM Oklahoma site, where the growing season

397　　extends well beyond that at most other sites, was substantially higher between GCC and GPP_{30}

398　　than between GCC and daily GPP (Table 2).

399

400　　For DBF and GRS, relationships between GPP and ExG were similar to those observed for GCC

401　　(Table 2). At ENF sites, correlations between ExG and GPP were marginally higher than those

402　　between GCC and GPP, but the magnitude of these differences was site-specific. At Wind River,

403　　in particular, ExG accounted for about 15% more variance in daily GPP than GCC because of

404　　the greater stability (less day-to-day noise) in ExG. Similar (but less pronounced) increases were

405　　also observed at Chibougamau, Howland, and Niwot.

406

407　　**Camera and flux-based phenophase transitions**

408　　Using a combination of greenness (GCC) and redness (RCC) indices, digital repeat photography

409　　facilitated accurate determinations of the start and end of the photosynthetic period for DBF and

410　　GRS. In ENF sites, however, the lack of a discernible winter baseline prevented accurate

411　　estimation of the start and end of canopy photosynthesis. In ENF and GRS, GCC provided a

412   relatively accurate estimation of the date of maximum photosynthesis; however, the relationship

413   in ENF was statistically insignificant. In the section below we elaborate on these themes,

414   discussing four camera-based phenology metrics – start of spring, middle of spring, middle of

415   fall, and end of fall – and their relationship with the seasonality of GPP.

416

417   At DBF sites, camera-derived spring and fall phenophase transition dates successfully captured

418   spatiotemporal variability in the beginning and end of the photosynthetic period. Start of spring,

419   estimated using Equation 4 fit to the GCC time series, was most highly correlated with the day of

420   year corresponding to when flux amplitudes were between 24-30% of maximum GPP ($R^2 = 0.62$;

421   n = 17). Mean deviation (MD) and RMSD between start of spring from GCC and GPP was

422   smallest at 20% and 24% of GPP amplitudes, respectively (Fig. 4a). Results were even stronger

423   (Fig. 4b) for the "middle of spring" (the date on which 50% of the seasonal amplitude in GCC

424   was reached), which corresponded to 30-40% of the spring amplitude in GPP ($R^2 = 0.82$). In

425   contrast, GCC was a relatively poor predictor of the date of maximum photosynthesis ($GPP_{90\%}$)

426   in DBF sites, with the date of $GCC_{90\%}$ consistently preceding the date of $GPP_{90\%}$ by more than

427   three weeks, on average. Note, however, that the magnitude of this bias was disproportionately

428   influenced by one site-year (Harvard Forest in 2010), in which a late summer increase in GPP

429   delayed the 90% threshold significantly (Fig. 5A).

430

431   Correlations between the date at which 50% of the seasonal amplitudes in GCC and GPP were

432   reached in fall was relatively weak ($R^2 = 0.43$; Fig. 4D). Similarly, correspondence between

433   GCC- and GPP-derived end of fall dates was also weak. Canopy redness (RCC), rather than

434   greenness, provided the best indicator of the end of the photosynthetically active period, with the

435   date of peak RCC strongly correlated to the date when GPP amplitude reached 14% ($R^2 = 0.69$;

436   Fig. 4c).

437

438   At GRS sites, GCC provided more information about seasonal dynamics in photosynthesis

439   during spring than in fall. GCC was a good indicator of the beginning of the photosynthetically

440   active period, with high correlation between both the start and middle of spring derived from

441   GCC time series and the date corresponding to a wide range of amplitudes in spring GPP (Fig.

442   6a, b). Relative to $GPP_{90\%}$, $GCC_{90\%}$ was less biased at GRS sites than that at DBF sites (Fig. 5c).

443   Similar to patterns observed in spring, the timing of both the middle and end of fall from GCC

444   showed significant (but lower relative to spring) correlations across a broad range of GPP

445   amplitudes (Fig. 6c).

446

447   At ENF sites, GCC typically started to increase prior to the onset of the growing season, when

448   GPP was still zero, and continued to decrease late in the year after GPP had returned to zero.

449   Thus, at both the start and end of the growing season, significant variations in GCC occur that

450   are not associated with dynamics in GPP. Indeed, correlations between the timing of changes in

451   GCC and GPP across a wide range of spring and fall amplitude thresholds (5–75% of seasonal

452   amplitude, in 5% intervals) were statistically insignificant at $p \leq 0.05$. It would appear, therefore,

453   that camera-based GCC time series cannot be used to predict the beginning or end of the

454   photosynthetically active period for ENF sites. It is worth noting, however, that GCC did provide

455   a rough indication of the date of maximum GPP. While the correlation between the dates on

456   which 90% of the spring amplitudes in GCC and GPP were reached was statistically insignificant

457   ($R^2 = 0.32$, p = 0.11), the mean bias (across all site-years) was less than one day (0.3 ± 10 d).

19

458

Integrated GCC and GPP

460   In the final element of our analysis, we investigated whether spring and fall time-integrated sums

461   of daily GCC provide additional or complementary information regarding interannual variation

462   in GPP relative to phenophase transition dates estimated from the GCC time series. To do this,

463   we first focused on the Barlett Forest site and calculated springtime integrated daily GPP and

464   GCC from 2006 to 2012 (Fig. 7). Starting on DOY 115 (selected to precede the earliest observed

465   green-up day, DOY 118), we integrated both GCC and GPP over successively longer time

466   segments at 5-day increments (e.g., DOY 115-120, 115-125, etc.). Results from this analysis

467   showed that springtime integrated GCC anomalies were strongly and significantly correlated

468   with integrated GPP anomalies for up to 30 days ($R^2 = 0.56$-0.88; n = 7), by which time

469   cumulative photosynthetic uptake had reached nearly 150 g C m^{-2} in some years. GCC and GPP

470   integrals beyond DOY 145 did not show statistically significant correlations. In fall, integrated

471   GCC anomalies computed for time segments spanning 30 days preceding the end of fall (DOY

472   290) were moderately correlated with corresponding GPP anomalies ($R^2 = 0.47$; p = 0.09; data

473   not shown). For comparison, start- and middle-of-spring transition dates were modestly

474   correlated with integrated GPP anomalies over the period from DOY 115 to 145 ($R^2 = 0.69$ and

475   0.43), while GCC-based middle and end-of-fall transition dates were highly correlated with time

476   integrals of GPP over the period from DOY 265 to 290 ($R^2 = 0.96, 0.70$). Thus, at Bartlett, GCC

477   integrals provide more information about flux anomalies than do individual phenological

478   transition dates in the spring, but less information in the fall.

479

480 We then extended this analysis to include all DBF and three of the four Illinois GRS sites (we

481 excluded the UI Maize and UI Soy notes, for which only a single year of data was available). For

482 the DBF sites, we found moderate correlation (as high as $R^2 = 0.49$; n = 19 after 30 days)

483 between normalized GCC integral anomalies and normalized GPP integral anomalies up to 60

484 days after green-up (Fig. 8). Over this period, anomalies of up to 158 gC m^{-2} (Harvard), or ~8%

485 of the annual total GPP, were observed. Correlations based on time integrals extending beyond

486 60 days after the earliest green-up were not statistically significant. In contrast to results at

487 Bartlett Forest, start- and middle-of-spring transition date anomalies were more highly correlated

488 with normalized GPP integral anomalies ($R^2 = 0.71$ and 0.60 at 20 and 30 days, respectively). In

489 fall, correlations between GCC integral anomalies and GPP anomalies were not statistically

490 significant, whereas end-of-fall transition date anomalies were weakly correlated with

491 normalized GPP integral anomalies ($R^2 = 0.30$). Multiple linear regression analysis showed that

492 about half the variance in annual GPP integral anomalies is explained by a combination of spring

493 and fall GCC anomalies ($R^2 = 0.54$). By comparison, a linear model using anomalies in the start-

494 of-spring and end-of-fall transition dates determined from the GCC time series explained less

495 than one-third of the variance in annual GPP integral anomalies ($R^2 = 0.30$). Thus, it is not clear

496 whether integrated GCC provides more information related to interannual variation in GPP than

497 specific transition dates.

498

499 At GRS sites we found strong correlation between normalized GCC anomalies and normalized

500 GPP anomalies up to 60 days after the start of spring ($R^2 = 0.97$; n = 6; Fig. 9) and during the

501 period 20-50 days preceding the end of the growing season ($R^2 = 0.83$). While these results are

502 promising, it is important to note that the sample size is small (n = 6) and each tower is

503 represented by only two site-years. As at DBF sites, information related to interannual variation

504 in fall GPP from time-integrated GCC values was comparable to that provided from transition

505 dates, but provided less information related to spring GPP variations. For example, correlation of

506 start-of-spring with spring GPP anomalies was lower than that for GCC anomalies ($R^2 = 0.85$)

507 while correlation of end-of-fall with fall GPP anomalies ($R^2 = 0.81$) was equivalent to that of the

508 integrated GCC anomaly.

509

510 **DISCUSSION**

511 **Canopy development and photosynthesis**

512 Results from this study demonstrate that canopy greenness is correlated with rates of

513 photosynthesis in both forest and grassland. Consistent with results from previous studies,

514 canopy greenness and GPP were correlated across DBF sites (Ahrends et al. 2009, Richardson et

515 al. 2007, 2009). For reasons that are unclear, we found a stronger relationship between

516 greenness and photosynthesis in grassland than Migliavacca et al. (2012). At ENF sites, our

517 results are consistent with those obtained by Richardson et al. (2009b) and showed moderate to

518 strong correlation between canopy greenness and GPP across all of the sites we examined. This

519 was particularly true for ExG, suggesting that camera-based modeling of GPP in ENF should be

520 based on this index. Specifically, ExG was less sensitive than GCC to variation in illumination

521 conditions. Thus, ExG appears to minimize the impact of shadows, which are prominent and

522 highly variable in conifer canopies.

523

524 Our analysis also revealed several limitations of canopy greenness as a predictor of GPP. For

525 example, there was a pronounced peak in GCC at the end of spring in DBF sites (also noted by

22

526   Sonnentag et al. 2012, Mizunuma et al. 2012) that preceded the peak in GPP by several weeks.

527   Peak GCC is caused by seasonal variation in foliage pigments (e.g., Sims and Gamon, 2002) and

528   is accentuated by the oblique viewing angle used by the cameras in this study (Keenan et al.

529   2014). As a result, $GCC_{90\%}$ tended to occur several weeks before $GPP_{90\%}$. Data from the

530   Missouri Ozarks site also demonstrated limitations of GCC during drought conditions when

531   photosynthesis was reduced by moisture stress, but canopy color was unaffected. As a result,

532   GPP and GCC became decoupled as GPP dropped rapidly while GCC remained high (Appendix

533   B). Even though ENF sites exhibited well-defined seasonality in greenness, GCC was only

534   weakly correlated to GPP at these sites. Conifers undergo seasonal changes in chlorophyll

535   content, with winter minima approximately 40% lower than summer maxima (Billow et al. 1994,

536   Ottander et al. 1995). Hence, seasonal variation in chlorophyll concentrations at sites with long

537   winters (Chibougamau, Groundhog, Niwot) may be driving observed patterns in canopy

538   greenness, even during the non-photosynthetic period (Fig. 2; Appendix C).

539

540   **Phenophase transitions and integrated GCC-GPP**

541   Start of spring and end of fall, determined based on GCC and RCC, provided biased estimates

542   for the beginning and cessation of the photosynthetically active period (*i.e.* GPP > 0 g C m^{-2} d^{-1}).

543   In deciduous broadleaf forest and grassland/crops sites, the MD and RMSD for the start of spring

544   were lowest for GPP values between 20-26% of the spring amplitude, while for end of fall,

545   deviations were lowest for GPP at 14-16% of the fall amplitude. Local maxima in the change in

546   curvature rate, which is used to identify the start of spring and end of fall (Zhang et al. 2003),

547   occurs above wintertime minimum values, when GCC reach ~10% and 90% of the amplitude of

548   equations 3 and 4, respectively. In DBF, an additional source of disagreement between the

23

549   timing of GCC and GPP is early season photosynthesis from sub-dominant evergreen trees,

550   which can increase ecosystem GPP well before leaf emergence in deciduous trees.

551

552   Garrity et al. (2011) tested 13 metrics of canopy phenology (excluding cameras) and found that

553   no single source provided adequate characterization of the full seasonality of carbon flux

554   phenology. Notably, the beginning of the photosynthetic period was generally well characterized

555   while the end of the photosynthetic period was poorly characterized, and the timing of maximum

556   GPP was not significantly correlated with any radiometric or remotely sensed variable (Garrity et

557   al. 2011). Although we found similar patterns for DBF sites, there was relatively close

558   association between $GPP_{90\%}$ and $GCC_{90\%}$ in GRS. Other researchers have found that maximum

559   GCC at DBF sites precedes maximum GPP (Ahrends et al. 2009, Richardson et al. 2009b), leaf

560   area index (Keenan et al., 2014), and leaf chlorophyll content (Nagai et al. 2011) by several

561   weeks to two months. Likewise, leaf-level studies indicate long periods (50-80 days) between

562   green-up and maximum photosynthesis (Reich et al. 1991, Bassow and Bazzazz 1998, Morecroft

563   et al. 2003). Thus, it is perhaps not surprising that we found that changes in GCC tend to lead

564   changes in GPP in both spring and autumn in DBF.

565

566   A particularly important conclusion from this work is that repeat digital photography not only

567   allows us to identify when photosynthesis begins and ends, but also helps us estimate how much

568   of an impact phenological variability has on seasonal and annual carbon budgets. Using an

569   independent measure of canopy phenology, we showed how changes in the timing of green leaf

570   phenology in the spring and fall affects cumulative photosynthesis. Among DBF sites, we also

571   found significant correlation between combined spring-fall GCC anomalies and anomalies in

572   annual GPP.

573

574   **Impacts and future work**

575   By examining relationships between camera-derived metrics of greenness and GPP across a large

576   set of sites spanning multiple years and three plant functional types, this research provides an

577   improved foundation for using digital repeat photography to model the impact of phenological

578   dynamics on the carbon cycle of terrestrial ecosystems. Key contributions of this study are (1)

579   demonstration of relatively general relationships between GPP and GCC, and (2) quantification

580   of spatiotemporal variability in canopy development and GPP among and across three major

581   PFTs. More generally, results from this study highlight the role that cameras can play in refining

582   and calibrating phenological sub-routines in Earth System models, which vary widely in their

583   representation of green leaf phenology (e.g., Richardson et al. 2012). The Community Land

584   Model, for instance, includes seven PFTs (Bonan et al. 2002), four of which were represented in

585   our study: deciduous broadleaf forest (DBF), coniferous evergreen forest (ENF), grasses (GRS),

586   and crops (GRS). Our study did not include broadleaf evergreen forest, deciduous and evergreen

587   shrubs, and we are not aware of any studies that have compared camera-based phenology and

588   carbon fluxes in broadleaf evergreen forest, (but see Doughty and Goulden 2007 for radiometry-

589   based phenology). However, given the major role of humid tropical forest in the global carbon

590   cycle, there is a clear need for camera-based studies in this biome.

591

592   Although our study was focused on canopy-scale phenology, digital repeat photography also has

593   significant potential as a tool for bridging the gap between canopy-to-landscape scale processes

25

594   and organismal-level observations of leafing and flowering phenology. Digital repeat

595   photography can also play an essential role in scaling organismal- and canopy-level observations

596   to the synoptic scale provided by remote sensing (Hufkens et al. 2012). As networks of spatially

597   referenced online camera imagery rapidly expand (Graham et al. 2010, Sonnentag et al. 2012,

598   Abrams and Pless 2013), opportunities to leverage these networks to monitor and calibrate

599   models of terrestrial phenology are likely to increase. Exploiting this, future work will explore

600   how such camera networks can be used to characterize spatiotemporal variability in phenology

601   and determine the environmental drivers (e.g. temperature, precipitation, photoperiod, snow

602   cover) that regulate canopy development and senescence at regional to continental scales.

603

604   **CONCLUSIONS**

605   In this study, we demonstrate the strengths and limitations of camera-based canopy greenness for

606   monitoring the phenology of photosynthesis in three PFTs: deciduous broadleaf forest, evergreen

607   needleleaf forest and grassland/crops. We encountered key differences among PFTs in the

608   relationship between canopy development, expressed as greenness, and the seasonality of carbon

609   fluxes. These differences were also evident in the detection of discrete phenophase transitions.

610   Canopy greenness proved effective at detecting the beginning and end of the photosynthetically

611   active period in GRS sites. In DBF sites, greenness was effective for detecting the beginning of

612   the photosynthetic period, whereas redness was most effective for detecting the end. A key

613   finding of this study was that integrated GCC was significantly correlated with total GPP during

614   the first 30-60 days following green-up, in both DBF and GRS. In some cases, integrated GCC

615   was a better predictor of summed spring/fall GPP than discrete transitions dates. Further, in DBF

616   there was a moderate correlation between combined spring-fall GCC anomalies and the annual

617   GPP integral anomalies, indicating significant seasonal control of shifts in phenology on

618   ecosystem productivity. Camera data thus provide a valuable and independent means by which

619   ecosystem-scale phenology can be characterized (cf. phenological metrics derived from CO_2

620   fluxes themselves, as in Richardson et al. 2010). Finally, our results suggest that digital repeat

621   photography may be used to estimate interannual variability in GPP resulting from phenological

622   variability with greater accuracy than many existing ecosystem process models provide (Keenan

623   et al. 2012, Richardson et al. 2012).

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Appendices

Appendix A. Map of PhenoCam sites.

Appendix B. Time series of daily GPP (gC m^{-2} d^{-1}) and GCC for all deciduous broadleaf forest (DBF) evergreen needleleaf forest (ENF) and grassland (GRS) sites, listed by plant functional type. One characteristic year of data is featured in each sub-plot.

Appendix C. Scatter plots of daily GPP (gC m^{-2} d^{-1}) vs. GCC for all deciduous broadleaf forest (DBF) evergreen needleleaf forest (ENF) and grassland (GRS) sites, listed by plant functional type. Linear (blue) and quadratic regression lines (red) are superimposed (see Table 2 for coefficients of determination). All years of data are featured in each sub-plot.

972   Table 1. Summary of camera/eddy covariance sites used in this study, arranged by plant functional type. DBF = broadleaf deciduous

973   forest, ENF = evergreen needleleaf forest, GRS = grassland/crops.

Site	PFT	Lat.	Long.	Alt. (m)	Years	Camera	Citation
Bartlett	DBF	44.0646	-71.2881	268	2006-2012	Axis 211	Richardson et al. 2007
Harvard	DBF	42.5378	-72.1715	340	2008-2011	StarDot NetCam SC	Urbanski et al. 2007
Missouri Ozarks	DBF	38.7441	-92.2000	219	2007-2008	Olympus D-360L	Yang et al. 2010
Morgan Monroe	DBF	39.3231	-86.4131	275	2009-2010	StarDot NetCam SC	Schmid et al. 2000
U Michbio1	DBF	45.5598	-84.7090	225	2008-2011	StarDot NetCam SC	Nave et al. 2011
U Michbio2	DBF	45.5598	-84.7138	230	2009-2011	StarDot NetCam SC	Curtis et al. 2002
Chibougamou	ENF	49.6924	-74.3420	380	2008-2010	StarDot NetCam SC	Bergeron et al. 2006
Groundhog	ENF/DBF	48.2174	-82.1555	350	2008-2011	StarDot NetCam SC	McCaughey et al. 2006
Howland	ENF	45.2041	-68.7403	80	2010-2012	Stardot NetCam SC	Hollinger et al. 1999
Niwot	ENF	40.0328	-105.5470	3055	2008-2011	Canon VB-C10R	Sacks et al. 2007
Wind River	ENF	45.8213	-121.9521	371	2011	StarDot NetCam SC	Wharton et al. 2012
ARM Oklahoma	GRS	36.6970	-97.4888	316	2003-2011	Nikon Coolpix 990	Torn et al. 2010

UI Maize/Soy	GRS	40.0628	-88.1961	314	2009-2010	Axis 211M	Zeri et al. 2011
UI Miscanthus	GRS	40.0628	-88.1984	314	2009-2010	Axis 211M	Zeri et al. 2011
UI Prairie	GRS	40.0637	-88.1973	314	2009-2010	Axis 211M	Zeri et al. 2011
UI Switchgrass	GRS	40.0637	-88.1973	314	2009-2010	Axis 211M	Zeri et al. 2011
Vaira	GRS	38.4133	-120.9506	129	2009-2010	D-Link DCS-900	Baldocchi et al. 2004

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989 **Table 2**. Coefficients of determination for linear (R^2) and quadratic regression (R^2_{quad}) of GCC

990 and ExG with daily GPP and mean 30-minute GPP rate (GPP_{30}). N = number of observations. In

991 all reported correlations, $p < 0.0001$.

Site	PFT	GCC-GPP_d		GCC-GPP_{30}		ExG-GPP_d		N
		R^2	R^2_{quad}	R^2	R^2_{quad}	R^2	R^2_{quad}	
Bartlett	DBF	0.782	0.783	0.765	0.773	0.787	0.793	740
Harvard	DBF	0.787	0.809	0.754	0.781	0.710	0.720	428
Missouri Ozarks	DBF	0.498	0.571	0.496	0.551	0.340	0.517	116
Morgan Monroe	DBF	0.629	0.680	0.618	0.706	0.623	0.680	221
U Michbio1	DBF	0.776	0.776	0.794	0.800	0.791	0.792	333
U Michbio2	DBF	0.788	0.819	0.771	0.794	0.415	0.456	356
Chibougamou	ENF	0.723	0.794	0.728	0.792	0.754	0.888	293
Groundhog	ENF/DBF	0.756	0.833	0.754	0.840	0.747	0.789	276
Howland	ENF	0.714	0.735	0.758	0.779	0.769	0.794	310
Niwot	ENF	0.654	0.675	0.707	0.714	0.707	0.761	169
Wind River	ENF	0.527	0.529	0.498	0.547	0.743	0.747	70
ARM Oklahoma	GRS	0.547	0.597	0.648	0.751	0.591	0.629	142
UI Maize	GRS	0.837	0.838	0.874	0.875	0.837	0.837	120
UI Miscanthus	GRS	0.861	0.870	0.872	0.888	0.811	0.828	243
UI Prairie	GRS	0.901	0.916	0.887	0.911	0.892	0.897	238
UI Soy	GRS	0.820	0.822	0.823	0.824	0.786	0.798	120
UI Switchgrass	GRS	0.805	0.815	0.789	0.808	0.749	0.764	243
Vaira	GRS	0.793	0.815	0.759	0.763	0.728	0.815	195

Figures

993 **Figure 1.** Examples of webcam photographs, representing the three plant functional types: (a)

994 Harvard (deciduous broadleaf forest), (b) Chibougamau (evergreen needleleaf forest), and (c) UI

995 miscanthus (grassland). Polygons indicate the Region of Interest for extracting image greenness.

996 **Figure 2.** Time series of daily GPP (blue circles, gC m^{-2} d^{-1}) and GCC (green diamonds) for

997 deciduous broadleaf forest (DBF; a) evergreen needleleaf forest (ENF; b) and grassland/crops

998 (GRS; c). Two characteristic years of data are featured in each sub-plot.

999 **Figure 3**. Scatter plots of daily GPP (gC m^{-2} d^{-1}) vs. GCC for deciduous broadleaf forest (DBF;

1000 a) evergreen needleleaf forest (ENF; b) and grassland (GRS; c). Linear (blue) and quadratic

1001 regression lines (red) are superimposed (see Table 2 for coefficients of determination). All years

1002 of data are featured in each sub-plot.

1003 **Figure 4**. Four metrics comparing estimates of DOY for start of spring (a), middle of spring (b),

1004 and middle of fall (d) using dates extracted from GCC curve fitting and % of maximum GPP.

1005 The plots represent 19 DBF site-years. End of fall (c) camera dates are derived from date of

1006 maximum RCC. On left axes, R^2 (0.0 – 1.0) and slope for geometric mean regression. On right

1007 axes, mean deviation (MD) and root mean square deviation (RMSD) of estimates; units are days.

1008 **Figure 5**. Comparisons of derived dates (DOY) of maximum greenness and fluxes – GCC$_{90\%}$

1009 and GPP$_{90\%}$, respectively – for deciduous broadleaf forest (a), evergreen needleleaf forest (b) and

1010 grassland/crops (C) sites.

1011 **Figure 6.** Four metrics comparing estimates of DOY of start of spring (a), middle of spring (b),

1012 end of fall (c) and middle of fall (d) using dates extracted from GCC curve fitting and % of

1013 maximum GPP. Plots represent 8 GRS site-years. On left axes, R^2 and slope for geometric mean

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1014   regression. On right axes, mean deviation (MD) and root mean square deviation (RMSD) of

1015   estimates; units are days.

1016   **Figure 7.** Regression of GPP integrated sums (gC m^{-2}) vs. GCC integrated sums (dimensionless)

1017   during the first 30 days following green-up (in 5-day increments) for 2006-2012 at Bartlett.

1018   **Figure 8**. Regression of GPP integrated sums (dimensionless) vs. GCC integrated sums

1019   (dimensionless) during the first 60 days following green-up (shown in 10-day increments) for

1020   deciduous broadleaf sites. Legend colors are equivalent to Figure 5a.

1021   **Figure 9**. Regression of normalized GPP integrated sums (dimensionless) vs. GCC integrated

1022   sums (dimensionless) during the first 60 days following green-up (in 10-day increments) for the

1023   GRS sites, UI Miscanthus (black circles), UI Prairie (white circles) and UI Switchgrass (grey

1024   circles).

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a. Harvard Forest Webcam Mon Jul 20 08:31:41 2009 EST Exposure: 200
Camera temp 58.0 °C Air temp 24.5 °C
RH 0%   Pressure 982.0 mb

b. Chibougamau Webcam Tue Jun 01 10:32:36 2010 EST Exposure: 295
Camera temp 42.5 °C Air temp 12.0 °C
RH 0%   Pressure 967.0 mb

c.

Harvard (DBF)

Chibougamau (ENF)

UI Prairie (GRS)

Harvard (DBF)

Chibougamau (ENF)

UI Prairie (GRS)

DOY 115 to 120

R^2=0.773
p=0.009

GPP integral (gC m^{-2})
GCC integral

DOY 115 to 125

R^2=0.791
p=0.007

GPP integral (gC m^{-2})
GCC integral

DOY 115 to 130

R^2=0.881
p=0.001

GPP integral (gC m^{-2})
GCC integral

DOY 115 to 135

R^2=0.831
p=0.004

GPP integral (gC m^{-2})
GCC integral

DOY 115 to 140

R^2=0.614
p=0.036

GPP integral (gC m^{-2})
GCC integral

DOY 115 to 145

R^2=0.567
p=0.050

GPP integral (gC m^{-2})
GCC integral