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

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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

66 **Keywords:** PhenoCam, digital repeat photography, phenology, photosynthesis, gross primary
67 productivity, seasonality, deciduous broadleaf forest, evergreen needleleaf forest, grassland

68 INTRODUCTION

69 Climate change impacts on vegetation phenology have been widely documented across a range
70 of biomes and plant functional types (Richardson et al. 2013). In particular, long-term records of
71 leaf and flower phenology in temperate and boreal forest indicate that spring onset is occurring
72 earlier (Miller-Rushing and Primack 2008, Thompson and Clark 2008, Aono and Kazui 2009,
73 Linkosalo et al. 2009), and more generally, that growing seasons are becoming longer on decadal
74 to millennial scales (Menzel 2000). Studies using satellite remote sensing have documented
75 trends towards longer growing seasons over large regions of in mid- and high-latitude
76 ecosystems of the Northern Hemisphere (Myneni et al. 1997, Zhang et al. 2007, Jeong et al.
77 2011, Xu et al. 2013). At lower latitudes, warmer temperatures have led to earlier spring
78 phenology and longer growing seasons in Mediterranean ecosystems (Penuelas et al. 2002,
79 Gordo and Sanz, 2010), while desert plant communities have experienced shifts in species
80 composition in response to changes in the timing of winter precipitation (Kimball et al. 2010).

81
82 While a large number of studies have identified widespread patterns of change, the impacts of
83 changes in phenology on ecosystem function and feedbacks to the climate system remain poorly
84 understood and quantified (Richardson et al. 2013). For example, multi-site comparisons show
85 that growing season length is positively correlated with net ecosystem productivity (NEP;
86 Churkina et al. 2005, Baldocchi 2008), but spatial patterns observed across sites are not identical
87 to temporal patterns at individual sites, which are driven primarily by interannual variability in
88 weather (Richardson et al. 2010). Warmer springs and longer growing seasons have been shown
89 to increase annual carbon uptake in boreal deciduous forest (Barr et al. 2004, 2007), mixed
90 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 Spectroradiometer (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 (Sonntag 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 Sonntag 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 Bader et al. 2011), desert shrublands (Kurc and Benton 2010), bryophyte communities (Graham
127 et al. 2006) and invasive plants (Sonntag 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 PFTs (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):

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

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:

$$208 \quad ExG = 2DN_G - (DN_R + DN_B) \quad (2)$$

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:

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

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

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
$$GCC(t) = a_1 + (b - a_2 \times t) \left(\frac{1}{1+e^{(c_s-d_st)}} - \frac{1}{1+e^{(c_f-d_ft)}} \right) \quad (4)$$

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 $(b - a_2 \times t)$. 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 ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) using the Q_{10} method (Raich and Schlesinger 1994):

$$262 \quad GPP = NEE - Reco = NEE - R_{ref} \times Q_{10}^{(T-T_{ref})/10} \quad (5)$$

263 where R_{ref} is a scaling parameter, Q_{10} is the temperature sensitivity of ecosystem respiration
264 (R_{eco}), and T_{ref} ($= 10^\circ$) 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 ($\text{g C m}^{-2} \text{ d}^{-1}$) 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 $\text{PPFD} \geq 5 \mu\text{mol m}^{-2} \text{ s}^{-1}$), as well as estimates of the light-

275 saturated rate of photosynthesis (A_{\max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), 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-](http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/)
281 [jena.mpg.de/~MDIwork/eddyproc/](http://www.bgc-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 ($\text{GPP} > 0 \text{ g C m}^{-2} \text{ d}^{-1}$) 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,

389 correlation between GCC and GPP₃₀ 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 GPP₃₀
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).

458

459 **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 $\sim 8\%$
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

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.* $GPP > 0 \text{ g C m}^{-2} \text{ d}^{-1}$).
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

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

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 CO₂
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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663 **LITERATURE CITED**

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937 **Appendices**

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939 **Appendix A.** Map of PhenoCam sites.

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

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

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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 |

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|----------------|-----|---------|-----------|-----|-----------|----------------|-----------------------|
| 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 |

992 **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, $\text{gC m}^{-2} \text{d}^{-1}$) 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 ($\text{gC m}^{-2} \text{d}^{-1}$) 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 – $\text{GCC}_{90\%}$
1009 and $\text{GPP}_{90\%}$, 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

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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