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1 **Title:** Cryptic phenology in plants: case studies, implications and recommendations

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4

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51 **Statement of authorship:**

52 LA organized and wrote the paper with advice/input from SMM, TEH and SRS. NRC  
53 contributed earth system model runs for the tropical forest case study at K67 and compiled  
54 comparison data into figures. MNS reviewed, synthesized and illustrated published LAI and  
55 litterfall data. For the temperate forest case study at Harvard Forest, SMM contributed DBH and  
56 allometry, and PC, AA, JM, WL, DMR, and XS contributed model runs and feedback on the  
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59

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61

62 **ABSTRACT**

63 Plant phenology – the timing of cyclic or recurrent biological events in plants – offers insight  
64 into the ecology, evolution, and seasonality of plant-mediated ecosystem processes. Traditionally  
65 studied phenologies are readily apparent, such as flowering events, germination timing, and  
66 season-initiating budbreak. However, a broad range of phenologies that are fundamental to the  
67 ecology and evolution of plants, and to global biogeochemical cycles and climate change  
68 predictions, have been neglected because they are “cryptic” – that is, hidden from view (e.g root  
69 production) or difficult to distinguish and interpret based on common measurements at typical  
70 scales of examination (e.g leaf turnover in evergreen forests). We illustrate how capturing cryptic  
71 phenology can advance scientific understanding with two case studies: wood phenology in a  
72 deciduous forest of the northeastern USA and leaf phenology in tropical evergreen forests of  
73 Amazonia. Drawing on these case studies and other literature, we argue that conceptualizing and  
74 characterizing cryptic plant phenology is needed for understanding and accurate prediction at  
75 many scales from organisms to ecosystems. We recommend avenues of empirical and modeling  
76 research to accelerate discovery of cryptic phenological patterns, to understand their causes and  
77 consequences, and to represent these processes in terrestrial biosphere models.

78

79 **1. INTRODUCTION**

80 All organisms have physical limits beyond which they function poorly or perish, and face trade-  
81 offs in the allocation of finite resources to different structures and functions (Araújo et al., 2013;  
82 Bennett & Lenski, 2007). Evolutionary strategies to establish, survive, grow, and reproduce are  
83 shaped by such fundamental constraints and trade-offs (Roff & Fairbairn, 2007; Stearns, 1989).  
84 When physical constraints or available resources vary regularly through time, organisms often  
85 evolve temporal patterns in their activities to match or complement these variations (Diamond,  
86 Frame, Martin, & Buckley, 2011). Temporal rhythms can also arise from time-dependent  
87 biological process such as ontogeny and demography (Niinemets, García-Plazaola, & Tosens,  
88 2012; Thomas & Winner, 2002). The Earth surface experiences seasonal cycles in temperature,  
89 precipitation, and light that influence the availability of resources and the potential to carry out  
90 the chemistry underlying biological processes (Schwartz, 2013; A. H. Strahler & Strahler, 2006).  
91 Sessile organisms, such as most multicellular plants, are subjected to these seasonal cycles in-  
92 place. Plant phenology—the timing of cyclic or recurrent biological events in plants—represents  
93 functional strategies to persist within the bounds of natural climate seasonality and biological  
94 possibility (Forrest & Miller-Rushing, 2010; Rathcke & Lacey, 1985). The study of phenology  
95 has thus long been used as a means for gaining insight into the ecology and evolution of plants  
96 and other organisms (Lieth, 1974).

97         The term ‘phenology’ traces to the Greek root *phaino*, meaning ‘to show,’ or ‘to appear’  
98 (Schwartz, 2013), and early influential works on phenology promoted observations of  
99 phenomena that were ‘sharp,’ ‘visible,’ and easy to detect (Leopold & Jones, 1947). In today’s  
100 lexicon, common definitions of phenology broadly encompass the timing of cyclic or recurrent  
101 biological events in plants, along with the causes and consequences of that timing (e.g. Lieth

1974, and (*phenology, n.* : *Oxford English Dictionary*, 2005). In contrast with broad contemporary definitions of phenology, studies of phenology often reflect the origin and history of the term by focusing on readily apparent biological events. These are generally aboveground and accompanied by changes that are readily and reproducibly distinguished with human senses such as visible changes in color, position, mass and volume. In plants, these include phenomena such as germination in annual plants, synchronized leaf production (leaf flush) and abscission in deciduous forests (Murali & Sukumar, 1993; Richardson & O’Keefe, 2009), and the onset of anthesis (flower opening) (Schwartz, 2013). Some phenological patterns, such as deciduous forest leaf onset, are also apparent at canopy and larger spatial scales with remote sensing tools ranging from phenocams to satellites (Badeck et al., 2004; Buitenwerf, Rose, & Higgins, 2015). Studying the timing and controls of such apparent biological events has contributed to understanding the evolution of plant traits and strategies in response to cycles in temperature, precipitation, photoperiod, and other physical variables (Chuine, 2010; Z. Huang, Liu, Bradford, Huxman, & Venable, 2016; Pau et al., 2011; van Schaik, Terborgh, & Wright, 1993). Phenological studies have also advanced our understanding of ecology, as many phenological patterns are coupled to biotic interactions such as intra-annual dynamics of predator or mutualist populations (Pau et al., 2011; Schwartz, 2013). More recently, some phenological events, such as date of anthesis or first leaf emergence, have proven useful indicators of biological responses to climate change (e.g. Parmesan & Yohe, 2003), and the relative ease of observing such events has enabled citizen science at regional and continental scales (Schwartz, Betancourt, & Weltzin, 2012).

However, many processes in plants are *not* readily apparent, but are no less cyclic or seasonal than the more easily observed phenomena that humans have historically monitored.

125 These phenologies are what might be called ‘cryptic.’ Some phenological patterns are difficult to  
126 detect because they are hidden, including below-ground activities such as allocation to roots, and  
127 internal processes such as allocation to carbohydrate reserves or cell differentiation. Other  
128 phenological patterns are missed or misinterpreted based on common measurements at typical  
129 scales of examination (e.g. changes in mass, area or volume of plant organs or of biomass pools).  
130 Cryptic phenologies are not as well understood as apparent phenologies, and they have not been  
131 used as indicators of climate change. Yet phenologies, including cryptic phenologies, play  
132 critical roles in ecosystems, and mediate large-scale fluxes of carbon, nutrients, water, and  
133 energy that are essential to consider as Earth’s climate changes (Abramoff & Finzi, 2015;  
134 McCormack, Adams, Smithwick, & Eissenstat, 2014; Noormets, 2009; Richardson, Keenan, et  
135 al., 2013b).

136 To address the disparity between the narrow scope of apparent phenology and the much  
137 broader scope of cyclic and seasonal plant activities, we first offer a framework with terminology  
138 that identifies the underlying challenges to observing, interpreting, and modeling cryptic  
139 phenologies. Then, focusing on trees, we review specific case studies in which missing cryptic  
140 phenology leads to problems for understanding and modeling seasonal ecosystem processes:  
141 wood allocation in a temperate mixed forest, and leaf phenology in tropical evergreen Amazon  
142 forests. We emphasize that attention to cryptic phenology is timely because many terrestrial  
143 biosphere models (TBMs, the models used to represent vegetation of the land surface in Earth  
144 system models and needed for climate change predictions; Fisher, Huntzinger, Schwalm, &  
145 Sitch, 2014), assume that cryptic phenologies are strongly correlated with apparent phenologies,  
146 and that such assumptions can lead to misattribution of the causes behind observed fluxes of  
147 carbon, water, nutrients, and energy. Although we focus on trees, we argue that cryptic

148 phenologies are ubiquitous, and their conceptualization, characterization, and interpretation are  
149 essential for accurate prediction at scales from organisms to ecosystems across the globe.

150 Table 1. Categorization of plant phenologies based on our current capacity for successful measurement, observation, and/or interpretation.

<b>Plant phenology category</b>	<b>Specific examples</b>	<b>Frequently measured?</b>	<b>Model representation examples</b>	<b>Examples of current or possible use</b>
<i>Apparent</i>				
Phases and events easily observed by humans.	<ul style="list-style-type: none"> <li>• Bud burst<sup>1</sup></li> <li>• Leaf abscission<sup>2</sup></li> <li>• Anthesis<sup>3</sup></li> <li>• Fruit maturation<sup>4</sup></li> </ul>	Yes, and some records extend for decades or longer.	May be prescribed by relying directly on observations to force the model (e.g. remote sensing indices), or may be simulated based on environmental controls (e.g. growing degree days). <sup>5</sup>	<ul style="list-style-type: none"> <li>• Defining the duration of the growing season in seasonally dormant systems.<sup>6,7</sup></li> <li>• Testing capacity of hydrothermal models to predict events such as germination.<sup>8,9</sup></li> <li>• Using changes in timing of phenological events as indicators of climate change.<sup>10,11,12</sup></li> </ul>
<i>Cryptic: hidden</i>				
Phases and events that are internal or obstructed by some barrier and thus difficult to detect.	<ul style="list-style-type: none"> <li>• Below-ground processes such as root production.<sup>13,14</sup></li> <li>• Structural changes within cells or tissues such as xylem formation.<sup>15</sup></li> <li>• Remote sensing in cloudy regions such as wet tropical forests.<sup>16</sup></li> </ul>	No, but these blind spots are generally acknowledged.	Often assumed to be linked to or dependent on apparent phenology. <sup>17,18</sup> This assumption is generally explicit.	<ul style="list-style-type: none"> <li>• Modeling of whole plant carbon and water dynamics.<sup>19,20</sup></li> <li>• Estimating intra-annual cycles of biomass gain.<sup>15</sup></li> <li>• Identifying temporal variation in below-ground interactions and associations.<sup>21,22</sup></li> </ul>
<i>Cryptic: ambiguous</i>				
Phases and events that are missed or misinterpreted due to summed variables or compensatory processes in the same variable.	<ul style="list-style-type: none"> <li>• Leaf quantity appears constant despite leaf turnover because new leaf production compensates for simultaneous old leaf abscission.<sup>23</sup></li> <li>• Bole diameter can be affected by both wood formation and water status.<sup>24</sup></li> </ul>	No, and these blind spots are not widely acknowledged. Measurements are needed at fine spatial or temporal scales, or with specialized tools, to capture and/or interpret the phenological pattern.	Often assumed to be represented by apparent phenology and/or assumed constant. These assumptions are generally implicit and often unrecognized.	<ul style="list-style-type: none"> <li>• Decomposing measurements into components that reveal phenological strategies.<sup>25,26</sup></li> <li>• Attributing cycles of ecosystem flux to endogenous versus exogenous drivers.<sup>27,28</sup></li> <li>• Resolving lagged responses from instantaneous responses and their relationship to periods of stress.<sup>29,30</sup></li> </ul>

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- <sup>1</sup> Budburst. (2019). Budburst: An online database of plant observations, a citizen-science project of the Chicago Botanic Garden. Glencoe, Illinois. <https://budburst.org/plant-groups>
- <sup>2</sup> (Escudero & Del Arco, 1987)
- <sup>3</sup> (Smith-Ramirez, Armesto, & Figueroa, 1998)
- <sup>4</sup> (Spellman & Mulder, 2016)
- <sup>5</sup> (Huntzinger et al., 2012)
- <sup>6</sup> (Churkina, Schimel, Braswell, & Xiao, 2005)}
- <sup>7</sup> (Schwartz, 2013)
- <sup>8</sup> (Bauer, Meyer, & Allen, 1998)
- <sup>9</sup> (Hardegree, 2006)
- <sup>10</sup> (Badeck et al., 2004)
- <sup>11</sup> (Schwartz, AHAS, & AASA, 2006)
- <sup>12</sup> (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007)
- <sup>13</sup> (Steinaker & Wilson, 2008)
- <sup>14</sup> (Radville, McCormack, Post, & Eissenstat, 2016)
- <sup>15</sup> (Cuny et al., 2015)
- <sup>16</sup> (Asner, 2001)
- <sup>17</sup> (Delpierre, Berveiller, Granda, & Dufrene, 2015)
- <sup>18</sup> (Abramoff & Finzi)
- <sup>19</sup> (Hu, Moore, Riveros-Iregui, Burns, & Monson, 2010)
- <sup>20</sup> (Michelot et al., 2012)
- <sup>21</sup> (Mullen & Schmidt, 1993)
- <sup>22</sup> (S. W. Simard et al., 2012)
- <sup>23</sup> (Albert et al., 2018)
- <sup>24</sup> (Chitra-Tarak et al., 2015)
- <sup>25</sup> (Tang & Dubayah, 2017)
- <sup>26</sup> (Smith et al. 2019)
- <sup>27</sup> (Wu *et al.*, 2016)
- <sup>28</sup> (Migliavacca *et al.*, 2015)
- <sup>29</sup> (Ogle *et al.*, 2015)
- <sup>30</sup> (Guo & Ogle, 2018)

## 152 2. THE CHALLENGE OF CRYPTIC PHENOLOGY: A FRAMEWORK

153 As discussed above, we describe *apparent* phenologies as those that were selected for clear  
154 observation by humans, often with minimal technological support. By contrast, *cryptic*  
155 phenologies require extensive investigation or validation to capture, and as a consequence have  
156 rarely been measured at the temporal or spatial scale necessary to document and understand  
157 (Table 1). ‘Cryptic’ is a useful term because it implies concealment and ambiguity—two general  
158 challenges to capturing and understanding the full scope of cyclic/recurrent biological events in  
159 plants. To highlight these challenges, here we frame cryptic phenology as ‘hidden’ or  
160 ‘ambiguous.’

161 Plant phenological patterns are *hidden* when some physical or technological barrier  
162 obstructs observation (Table 1). Soil conceals below-ground processes such as cycles of root  
163 production and turn-over (Abramoff & Finzi, 2015; Delpierre et al., 2016). Internal plant  
164 structures are (by definition) hidden behind layers of cells, making the timing of recurrent  
165 processes such as secondary xylem (wood) formation difficult to observe *in vivo* (Chaffey, 1999;  
166 Plomion, Leprovost, & Stokes, 2001). Large-scale phenological processes can also be hidden, as  
167 cloud cover can consistently obstruct satellite observations of vegetation reflectance over humid  
168 regions such as tropical forests (Asner, 2001). In dense forests, the upper canopy leaves partly  
169 obstruct remote sensing observations of mid- and understory leaf area patterns (Tang &  
170 Dubayah, 2017) and vice versa for ground-based observations, (Smith et al., 2019). When  
171 phenological processes are hidden, describing them often requires time-consuming methods,  
172 such as minirhizotrons or soil cores (for roots; Abramoff & Finzi, 2015; Gaudinski et al., 2010),  
173 fixation of tissue samples from multiple time periods (for wood formation; Arend & Fromm,  
174 2007), or ‘ground truth’ observations (for remotely-sensed vegetation greenness indices;

175 Chavana-Bryant et al., 2017; Lopes et al., 2016; Richardson et al., 2018; Wu et al., 2017).  
176 Hidden phenological patterns are challenging and/or time-consuming to measure, but the  
177 scientific community frequently acknowledges the scarcity of these measurements, and models  
178 including hidden phenology explicitly define their representation within allocation schemes (e.g.  
179 Abramoff & Finzi, 2015).

180 Phenological patterns in plants are *ambiguous* if phases and events are missed or  
181 misinterpreted due to summed variables or compensatory processes in the same variable (Table  
182 1). A measured variable (e.g. plant mass, canopy leaf area, or bole volume) may be a function of  
183 multiple variables that are not synchronized with each other (Fig. 1a), making it difficult to  
184 interpret the temporal changes in the measured variable. For example, determining whether  
185 changes in tree stem diameter are caused by long-term carbon gain (such as xylem wall  
186 thickening), or reversible changes in plant water status (such as stem expansion or shrinkage), is  
187 difficult solely on the basis of stem diameter measurements (Chitra-Tarak et al., 2015; Cuny et  
188 al., 2015; Sheil, 1997). Additional examples of ambiguous phenological patterns arise when, for  
189 a given system, there are inputs and outputs of the same variable that are compensatory,  
190 maintaining the appearance of constancy despite change. For example, compensatory leaf  
191 production and abscission could maintain a constant total quantity of leaves in the canopy,  
192 belying underlying cycles in leaf production and abscission (Albert et al., 2018; Doughty &  
193 Goulden, 2008; Wu et al., 2016). In this example, at least two of the three terms (inputs, outputs,  
194 and total) need to be sufficiently constrained by measurements to determine whether the steady  
195 state of the total is achieved due to *constant* inputs and outputs (Fig. 1b) versus cyclic, but  
196 *compensatory* inputs and outputs (Fig. 1c). Whatever the scale of study, measuring multiple

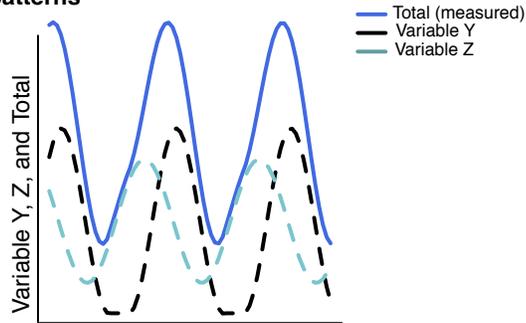
197 terms over time requires more effort and/or instrumentation, and this difficulty contributes to the  
198 challenge of recognizing and resolving ambiguous phenology.

199       Whereas hidden phenological patterns are often acknowledged to exist, but rarely  
200 measured, ambiguous phenological patterns are not frequently acknowledged because  
201 measurements *are* being made—the challenge lies in interpreting those measurements. For  
202 example, we understand that root phenology is hidden, and difficult to measure, because roots  
203 are underground. By contrast, we may not even realize that leaf production and loss show  
204 seasonal rhythms if the quantity of leaves in a canopy is largely constant (a compensatory  
205 scenario). The distinction between hidden and ambiguous categories is not absolute because  
206 phenology could be both hidden and ambiguous. For example, the mechanism of biomass gain  
207 (xylogenesis) is hidden within stems, and stem diameter represents an integration of cells at  
208 different stages in the sequence of xylogenesis: cell expansion, secondary cell wall thickening,  
209 lignification and dead cells (Cuny et al., 2015; Plomion et al., 2001). Thus changes in stem  
210 diameter emerge from expansion as well as biomass gain (Cuny et al., 2015), resulting in some  
211 ambiguity.

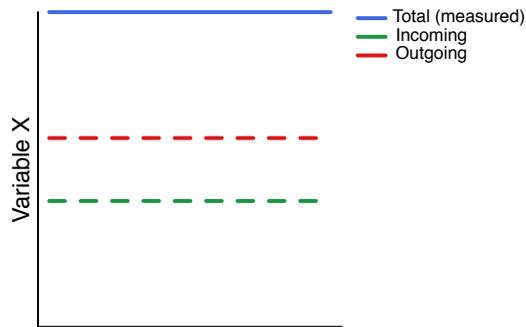
212       Cryptic phenologies do not follow fundamentally different rules than their more apparent  
213 counterparts. Plant phenologies, in general, are consequences of biology, climatic seasonality,  
214 and their interactions. Yet a focus on cryptic phenology challenges us to explicitly consider our  
215 current observational blind spots. These blind spots may prevent us from gaining a  
216 comprehensive understanding of organismal strategies and limitations in relation to their biology  
217 and physical environment, with consequences for our understanding of population, community,  
218 and ecosystem ecology. Ultimately, our ability to document, understand, and model the  
219 component processes that contribute to large-scale biosphere/atmosphere exchange of CO<sub>2</sub> and

220 water vapor, impacts our ability to predict responses of natural systems to global change (Getz et  
 221 al., 2017; Noormets, 2009; Richardson et al., 2012).

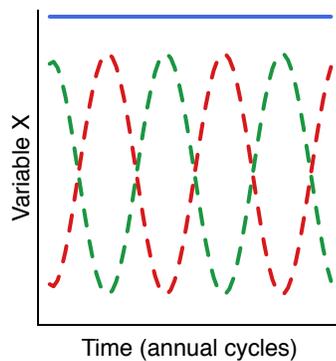
**(a) Example 1: Measured variable is the sum of multiple other variables with different temporal patterns**



**(b) Example 2: Measured variable is the sum of constant incoming and outgoing pools**



**(c) Example 3: Measured variable is the sum of compensatory incoming and outgoing pools**



222  
 223 Figure 1: Examples of ambiguous phenological patterns. In example 1, multiple variables (Y and  
 224 Z) contribute to some total that is measured. Variables Y and Z may have different peak timing,  
 225 different rates of change, and/or different amplitudes, that become summed for the measured total.  
 226 Thus the phenological patterns of individual variables Y and Z are ambiguous. In examples 2 and  
 227 3, the total for some biological variable X is the sum of an incoming (new) pool and outgoing (old)  
 228 pool. In example 2, the total, the incoming, and the outgoing pools are constant. In example 3, the

229 total is also constant, but the incoming and outgoing pools are dynamic, with inputs compensating  
230 for losses. Distinguishing between the scenarios represented by examples 2 and 3 is difficult based  
231 solely on measurements of the variable X total, and so phenological patterns of the incoming and  
232 outgoing pools remain ambiguous.

233

### 234 **3. CASE STUDIES IN CRYPTIC PHENOLOGY**

235 In the two case studies below, we draw upon available studies, data, and models to examine the  
236 evidence for, and implications of, cryptic phenology in two different plant processes in distinct  
237 ecosystems: allocation to wood in temperate deciduous forests, and gross primary productivity in  
238 tropical evergreen forests. For each case study we compare observations with simulations from  
239 terrestrial biosphere models (TBMs; models that represent land surface vegetation in the Earth  
240 system models used to simulate current and future global energy, carbon and water budgets  
241 (Fisher et al., 2014; Le Quéré et al., 2015). These model-observation comparisons serve two  
242 purposes. First, comparisons of TBMs with observations offer a test of our current ability to  
243 reproduce the seasonality of biosphere-atmosphere mass exchanges and represent phenological  
244 processes (Richardson et al., 2012) with implications for improving models (Richardson,  
245 Keenan, et al., 2013b). Second, the model-observation comparisons, placed in the context of  
246 current literature examining multiple scales and using multiple tools, allows us to ask whether  
247 cryptic phenology presents obstacles to our ability to test hypotheses about the drivers,  
248 consequences, and even the presence of phenology. Together, these case studies represent  
249 different plant organs and ecosystems, demonstrating how capturing cryptic phenological  
250 processes can be necessary for correct attribution of cause and effect—and ultimately modeling  
251 ecosystem processes—in many systems.

252

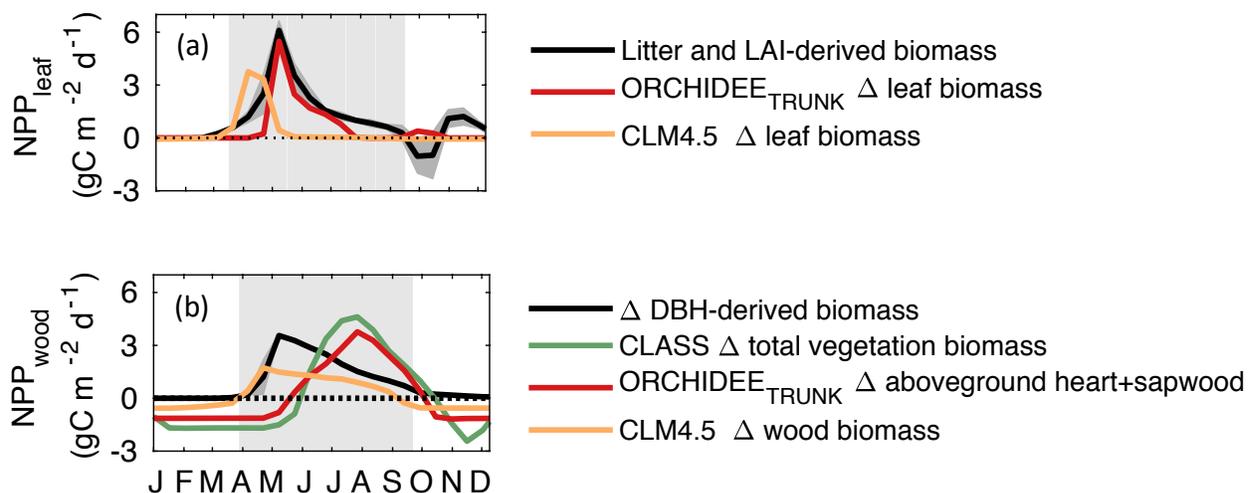
#### 253 **3.1 Cryptic phenology of bole growth in temperate forests: implications for the timing of**

254 **carbon allocation to wood**

255 A TBM model-data comparison of bole growth at Harvard Forest, a temperate mixed forest site,  
256 reveals the challenge of estimating and modeling the hidden phenology of biomass gain from  
257 wood allocation. Wood is a major component of aboveground biomass, and is important for  
258 characterizing fast versus slow growth strategies across species (Chave et al., 2009; Reich,  
259 2014). The intra-annual timing of wood allocation may show how carbon gain responds to  
260 seasonal climate, and reveal periods of vulnerability or resilience to stress (Babst et al., 2014;  
261 Battipaglia et al., 2010). The process of woody biomass gain (from xylogenesis) is hidden within  
262 boles (Cuny et al. 2015), and tree or plot scale biomass cannot be directly measured without  
263 harvesting trees (Clark & Kellner, 2012). Because of this, woody biomass gain is rarely  
264 measured (Cuny et al. 2015). Aboveground biomass change, which includes non-wood  
265 components such as leaves, can be estimated by measuring bole diameter growth increment for  
266 use with taxa-specific allometric equations (Chave et al., 2014; Chojnacky, Heath, & Jenkins,  
267 2014). This approach is used in both multi-year (e.g. McMahon, Parker, & Miller, 2010) and  
268 seasonal studies (McMahon & Parker, 2015; Delpierre et al., 2016).

269 We asked whether TBMs captured the phenology of carbon allocation to wood, and the  
270 phenology of carbon allocation to leaves, with equal success. We expected that TBMs would be  
271 challenged to capture the phenology of carbon allocation to wood because it is hidden and hence  
272 rarely measured at fine timescales, so there are few datasets available to improve, constrain, and  
273 test models (Delpierre et al., 2016). By contrast, carbon allocation to leaves is more apparent,  
274 particularly in forests with many deciduous tree species with spring leaf emergence and autumn  
275 senescence. We used fine scale changes in bole diameter growth as an estimation of the net  
276 primary productivity (NPP) allocated to wood ( $NPP_{\text{wood}}$ ). The allometric regression equations

277 were applied to a bi-weekly time series of high accuracy diameter at breast height (DBH)  
 278 measurements from dendrometer bands (McMahon & Parker, 2015) for three tree species at  
 279 Harvard Forest (supporting information appendix S1). We estimated NPP allocated to leaves  
 280 ( $NPP_{leaf}$ , Fig. 2a) at Harvard Forest based on leaf area index and litterfall time series (J. W.  
 281 Munger, n.d.; W. Munger & Wofsy, 2018; Urbanski et al., 2007; supporting information  
 282 appendix S2). Resulting  $NPP_{leaf}$  and  $NPP_{wood}$  reveal that carbon investment in leaves and wood is  
 283 highest early in the growing season (Fig. 2). The peaks in simulated  $NPP_{leaf}$  were within days of  
 284 the estimated peak  $NPP_{leaf}$  (and close to leaf budburst, which typically occurs around May 6  
 285 (Keenan and Richardson, 2015). By contrast, simulated phenological patterns in wood-related  
 286 output variables from three TBMs showed greater variation (Fig. 2, appendix S3). While the  
 287 Community Land Model version 4.5 (CLM4.5) shows a peak close to that seen in the  
 288 observations (around the time of budburst, at May 5), the peak for ORCHIDEE<sub>TRUNK</sub> and  
 289 CLASS are months later (August 1 and August 11 respectively).



290  
 291 Figure 2: Seasonality of observed (black  $\pm$  gray standard deviation) versus model-simulated  
 292 (colors) Net Primary Productivity (NPP) allocated to a) leaf biomass ( $NPP_{leaf}$ ), and b) woody  
 293 biomass ( $NPP_{wood}$ ) metrics at a mixed deciduous evergreen temperate forest.  $NPP_{leaf}$  observations  
 294 were calculated as  $(dLAI/dt) \cdot LMA + \text{litterfall}$  where LAI is leaf area index and LMA is leaf mass

295 per area. For models,  $NPP_{\text{leaf}}$  is calculated as the change in leaf biomass.  $NPP_{\text{wood}}$  observations  
296 were from allometry using diameter-at-breast-height (DBH) increment measurements compared  
297 with outputs from three land surface models. For models,  $NPP_{\text{wood}}$  was calculated as  $(X_i - X_{i-1}) / (t_i$   
298  $- t_{i-1})$  where  $X$  is the model output variable most comparable to aboveground woody biomass (in  
299  $\text{gC m}^{-2} \text{ day}^{-1}$ ) for each model (which was vegetation biomass for CLASS, aboveground heartwood  
300 plus sapwood for ORCIDEE<sub>TRUNK</sub>, and wood biomass for CLM4.5) and  $t$  is time in days. Temporal  
301 resolution is 16-day averages. The gray shaded area in all panels indicates the growing season, and  
302 the horizontal dotted line indicates zero.  $NPP_{\text{leaf}}$  simulations were not available for CLASS. Full  
303  $NPP_{\text{wood}}$  estimation and model details are available in online supporting information.

304 In interpreting this model-observation comparison, it is important to remember that using  
305 DBH with allometric scaling equations produces estimates—not direct measurements—of  
306 biomass (Clark & Kellner, 2012), and to consider that TBMs differ in how the wood pool is  
307 defined, which is not necessarily identical to aboveground woody biomass (see Table S1 and S2  
308 for model-specific definitions). In addition, there is some ambiguity in DBH-derived wood  
309 phenology because DBH represents multiple summed variables (Fig. 1a). DBH can be affected  
310 by changes in plant water status in addition to changes in biomass, and so seasonal changes in  
311 water availability could affect biomass estimations derived from allometry unless a correction is  
312 applied (Chitra-Tarak et al., 2015). The actual biomass gain (from xylogenesis) may also lag  
313 increases in DBH by weeks (Cuny et al., 2015). Explicit recognition of the distinction between  
314 measurable metrics (such as DBH) and the underlying variable we want to characterize or model  
315 (such as carbon biomass gain) motivates investigators to quantify uncertainty, and test for  
316 scenarios when proxies do not work well.

317 Despite the limitations of the observations and models, the comparison suggests that  
318 some models (like CLM 4.5) align moderately well with DBH-derived  $NPP_{\text{wood}}$ , while others lag  
319 DBH-derived  $NPP_{\text{wood}}$  by months. This divergence in model behaviors highlights the importance  
320 of understanding the mechanisms driving both simulated and observed phenologies. The timing  
321 of allocation to biomass and wood-related variables in these TBMs is primarily determined by  
322 the pattern of NPP across seasons. In ORCHIDEE for example, the allocation fractions to

323 different tissues primarily respond to environmental conditions: water, light, and nitrogen  
324 (Krinner et al., 2005). For the wood allocation in ORCHIDEE, a fraction of NPP is  
325 instantaneously allocated to sapwood, then sapwood biomass is converted into heartwood  
326 biomass based on a one-year time constant (Krinner et al., 2005). Ultimately, model NPP is  
327 controlled by site-specific climate conditions and representations of forest physiology (e.g. plant  
328 functional type), including leaf phenological patterns (e.g. leaf onset/abscission).

329         In contrast with model representations, physiological and tree-ring studies suggest that  
330 the mechanisms underlying wood phenology go beyond environmental controls to also include  
331 ontogeny of wood cells (Cuny et al., 2015; Plomion et al., 2001) and priorities in allocation  
332 through time (e.g. allocation of carbon to wood growth versus storage as nonstructural  
333 carbohydrates; Richardson, Carbone, et al., 2013a). Xylem production and differentiation follow  
334 a sequence, and shifts in one phase are associated with comparable shifts in successive phases  
335 (Rossi et al., 2013). This sequence offers a mechanism for wood phenology to respond to  
336 environmental conditions that are integrated over time—not just instantaneous drivers (Rossi et  
337 al., 2013). This sequence may also play a role in determining when trees are vulnerable or  
338 resilient to stress. For example, developing wood cells expand before their cell walls thicken  
339 with carbon-rich polysaccharides and lignins, and late wood is more dense than early wood in  
340 temperate species (Plomion et al., 2001), so trees at different stages in the sequence of wood  
341 development could be more or less sensitive to drought stress. Testing and developing model  
342 frameworks for such hypotheses is currently challenging because the timing of carbon allocation  
343 to wood is hidden *in vivo*. More direct measurements of wood formation (e.g. Cuny *et al.* 2016),  
344 and nonstructural carbohydrates (e.g. Newell, Mulkey, & Wright, 2002), synchronized with  
345 frequent measurements of DBH and leaf phenological patterns, would help us to understand and

346 model controls over wood phenological patterns (Delpierre et al., 2016; Guillemot et al., 2017),  
347 and how the timing of wood allocation relates to growth strategy, environmental fluctuations,  
348 and other plant traits.

349

### 350 **3.2 Amazon evergreen forests: implications of cryptic phenology for seasonality of** 351 **ecosystem carbon fluxes**

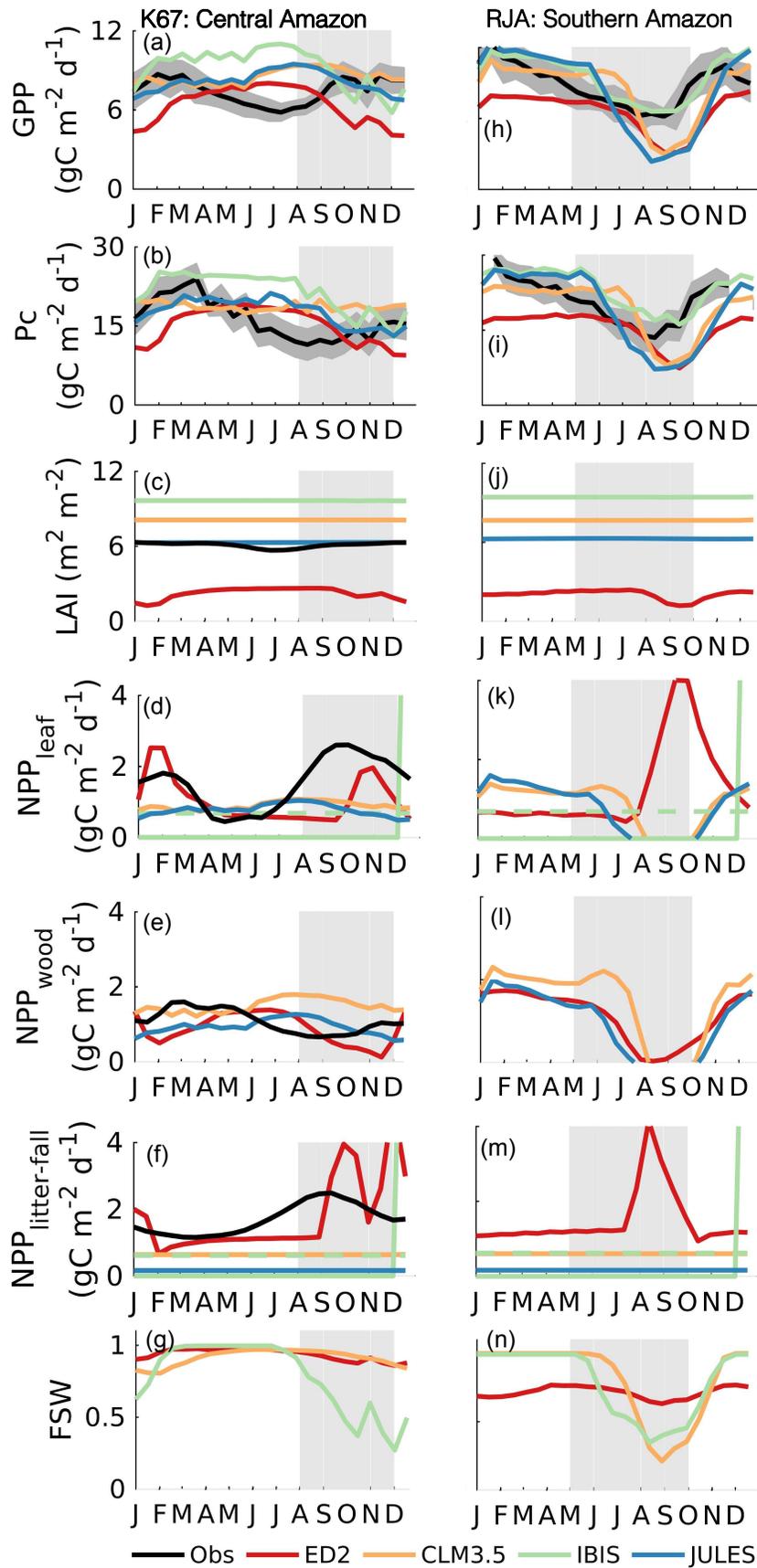
352 The challenge of cryptic phenology is not confined to a particular plant organ. Amazon  
353 evergreen forests near the equator offer a case study where leaf phenology is ambiguous. Much  
354 of the Amazon basin experiences annual wet and dry seasons (Restrepo-Coupe et al., 2013), and  
355 this regular seasonal variation in cloud cover and precipitation may select for phenological  
356 strategies that match plant activities with resource availability (Doughty et al., 2014; Graham,  
357 Mulkey, Kitajima, Phillips, & Wright, 2003; M. O. Jones, Kimball, & Nemani, 2014; van Schaik  
358 et al., 1993). Most of the Amazon is remote, making ground-based observations of phenology  
359 difficult, especially given the many observations needed to sample the high diversity of tree  
360 species (Cardoso et al., 2017) and strategies (Reich, 1995). Observations of canopies from  
361 satellites are often obstructed by clouds (Asner, 2001), difficult to interpret (Samanta et al.,  
362 2012), and the subject of controversy surrounding technical artifacts and their correction (Huete  
363 et al., 2006; Morton et al., 2014; Saleska et al., 2016). Yet many recent studies offer evidence  
364 that leaf production, leaf abscission, wood production and root production exhibit annual  
365 rhythms in Amazon forests (Doughty et al., 2014; Girardin, Malhi, & Doughty, 2016; Lopes et  
366 al., 2016; Wagner et al., 2016).

367 Many TBMs seem to be missing these phenological processes (Restrepo-Coupe et al.,  
368 2017). Evidence that TBMs are lacking adequate phenological representation comes from a

369 model inter-comparison for a network of ecosystem flux observations sites (eddy flux towers) in  
370 Amazonia (Restrepo-Coupe, et al., 2017). For illustration, we discuss the contrasting cases of  
371 equatorial versus southern evergreen forest sites in the Amazon basin of Brazil. At the equatorial  
372 site (K67 in the Tapajós National Forest, Brazil), four TBMs showed significant divergence from  
373 the estimated interannual pattern of whole-system photosynthetic fluxes (Fig. 3a, gross primary  
374 productivity, (GPP;  $\text{gC m}^{-2} \text{d}^{-1}$ ) and a metric of photosynthetic capacity, ( $P_c$ ;  $\text{gC m}^{-2} \text{d}^{-1}$ ) for K67;  
375 (Restrepo-Coupe et al., 2017). The reason for the divergence is that modeled photosynthetic  
376 patterns are driven by environmental variability -- measures of soil water stress in this case  
377 (model calculated soil water stress index 'FSW' for K67, Fig. 3b-g) -- which suppresses GPP  
378 during the long dry season. Yet the observed interannual pattern of photosynthesis in this  
379 ecosystem appears to be driven by something beyond instantaneous responses to seasonal  
380 climate fluctuations.

381         Since TBMs already include climatic seasonality, their failure to capture GPP seasonality  
382 suggests that phenological processes operate at the equatorial site that are separate from the  
383 instantaneous physiological responses already represented. Canopy phenological activity could  
384 drive the observed GPP via two mechanisms: 1) dry season increases in quantity of canopy  
385 leaves (quantified as leaf area index, or LAI) and/or 2) dry season increases in canopy  
386 photosynthetic capacity on a per unit area basis (Lopes et al., 2016; Restrepo-Coupe et al., 2017;  
387 Wu et al., 2016). Observations of leaf quantity (LAI) from equatorial Amazon sites show that  
388 LAI varies little across seasons (e.g. Fig. 3c 'LAI' shows low seasonality at K67). Leaf turnover,  
389 however, exhibits a dry season pulse (Fig. 3e,f: 'NPP<sub>leaf</sub>' and 'NPP<sub>litter-fall</sub>'), suggesting that LAI  
390 is maintained because leaf production compensates for near-simultaneous leaf fall during the dry  
391 season. As a result, LAI exhibits modest seasonal variation relative to seasonal variation in leaf

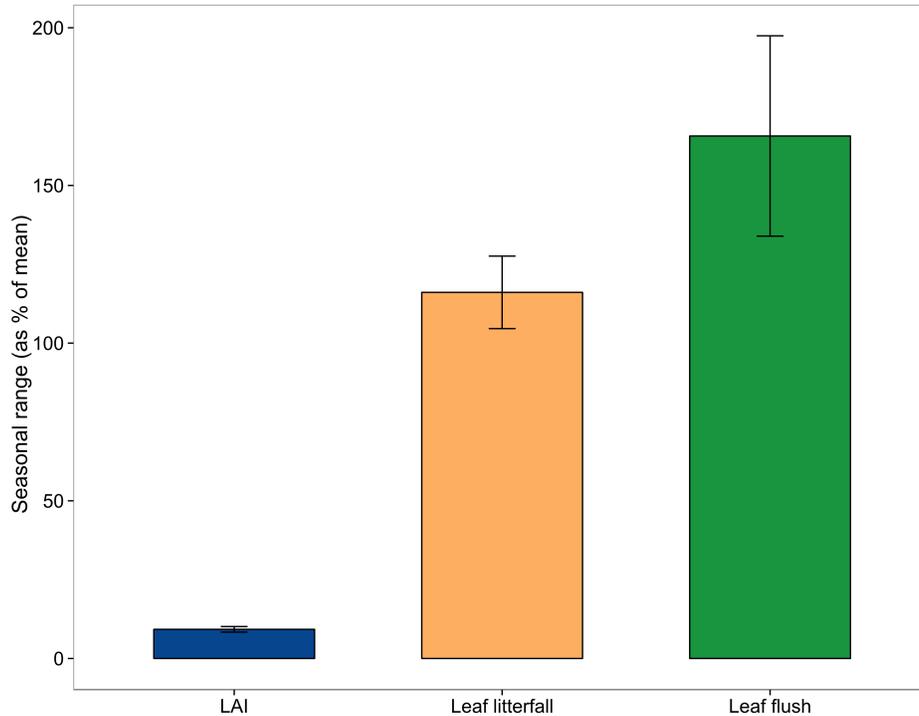
392 litterfall and leaf flush (Fig. 4). The seasonality of total LAI also fails to represent within-canopy  
393 dynamics, as compensatory leaf area patterns have been identified between the upper and lower  
394 canopy levels at K67 (Smith et al., 2019). Since new (recently expanded) leaves have high rates  
395 of photosynthesis, replacing old leaves with new leaves can increase photosynthetic capacity of  
396 the canopy on a per unit area basis (Albert et al., 2018; Doughty & Goulden, 2008; Niinemets et  
397 al., 2012; Pantin, Simonneau, & Muller, 2012; Wu et al., 2016).



399 Figure 3: Annual cycles of observed (black  $\pm$  gray standard deviation) versus model-simulated  
400 (colors) forest metrics in two Amazon forests (an equatorial Amazon forest, K67, and a southern  
401 Amazon forest, RJA), including (panels from top to bottom): daily average ecosystem-scale  
402 photosynthesis (GPP); daily average ecosystem-scale photosynthetic capacity (Pc, GPP at a fixed  
403 PAR range (725-875  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), vapor pressure deficit, air temperature and light quality  
404 measured as cloudiness index (all time mean  $\pm$  1 standard deviation)); leaf area index (LAI); net  
405 primary productivity (NPP) allocated to leaves (leaf production;  $\text{NPP}_{\text{leaf}}$ ); NPP going to litterfall  
406 ( $\text{NPP}_{\text{litterfall}}$ ), and NPP allocated to wood ( $\text{NPP}_{\text{wood}}$ ); soil water stress metric (FSW), where 1=no  
407 stress (Ju et al., 2006). The light gray shaded box all panels represents the dry season. For K67  
408 LAI data, we use data from the control plot of a close-by drought experiment (Juárez et al. 2007;  
409 Brando et al. 2010). LAI and NPP observations were not available for the RJA site. Lines are  
410 dashed for IBIS NPP to indicate that NPP is allocated only at the end of the year. For further details  
411 on model intercomparison, see Restrepo-Coupe et al. (2017).

412 The combination of leaf turnover and leaf age-dependent  $\text{CO}_2$  assimilation capacity creates a  
413 scenario at K67 in which ecosystem photosynthetic capacity varies more than LAI (Fig. 3b,c).  
414 Therefore, the observable canopy total LAI time series does not fully capture phenological  
415 patterns of leaf turnover or the resulting shifts in canopy photosynthetic capacity at this site (Fig.  
416 5) because leaf phenology is compensatory (Fig. 1c).

417 In contrast to the equatorial Amazon site, at a southern Amazon forest (Reserva Jarú,  
418 RJA), observations and models coincide, with GPP and Pc declining during the dry season,  
419 consistent with increasing water limitation as the dry season progresses (Fig. 3h,i,n). We lack an  
420 observational time series of LAI and litterfall for the southern site, but remote sensing (GLAS  
421 satellite lidar) suggests that in the southern Amazon, LAI decreases during the dry season (Tang  
422 & Dubayah, 2017). Thus the equatorial (K67) and southern (RJA) Amazon sites appear to  
423 include trees with different phenological strategies (Restrepo-Coupe et al., 2013). We  
424 hypothesize that many trees in high water availability equatorial sites may be adapted to optimize  
425 light use over time, synchronizing leaf production with the sunny dry season as a strategy for  
426 increasing annual carbon gain (Restrepo-Coupe et al., 2017). The tree communities at southern  
427 sites like RJA may experience a weaker peak in dry season sunlight (Restrepo-Coupe et al.,  
428 2013), and may shed leaves during dry seasons to protect plant water status.

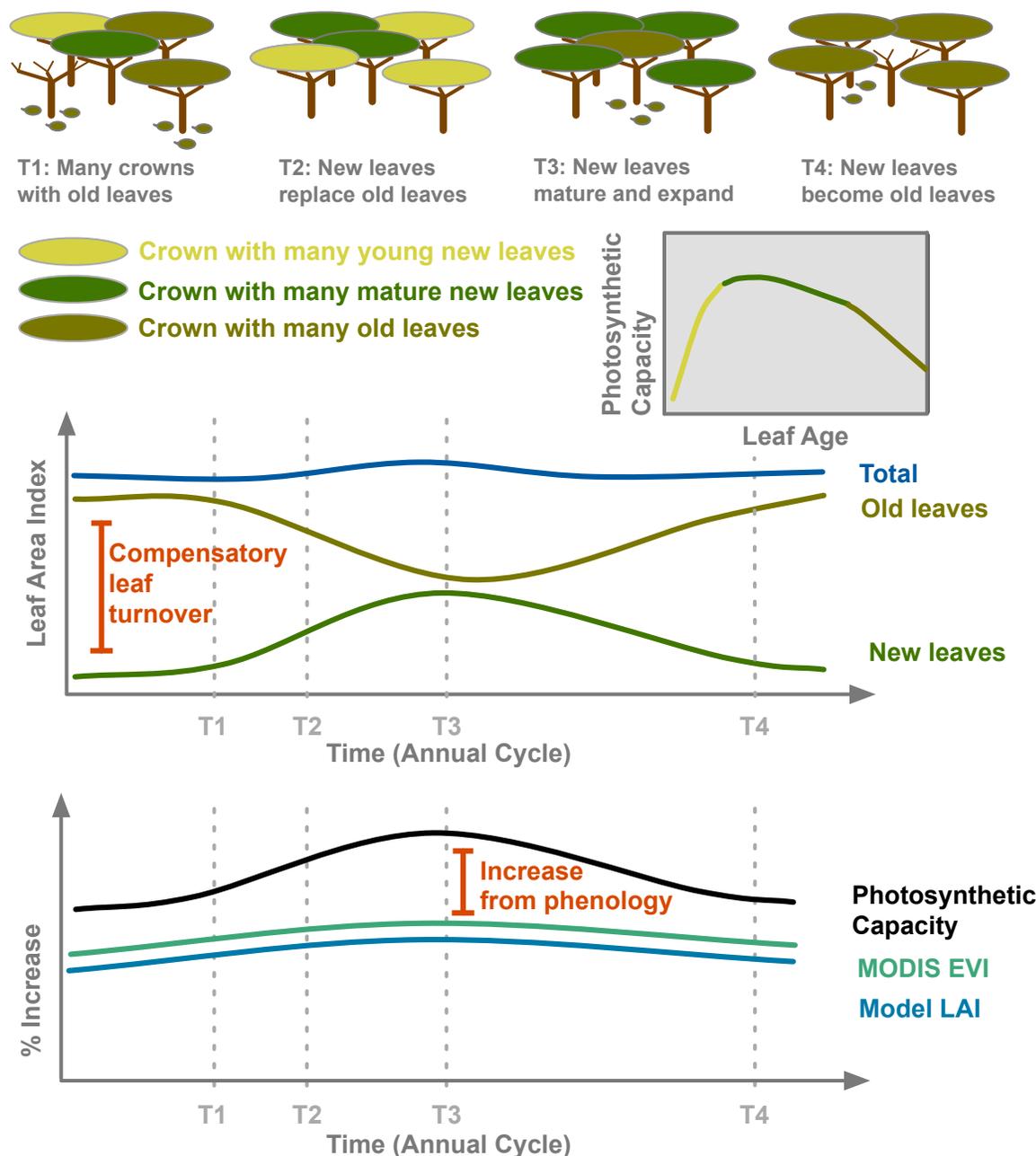


429

430 Figure 4: Seasonal canopy dynamics of Leaf Area Index (LAI), leaf litterfall, and leaf production  
 431 averaged across five Amazonian sites, showing that large leaf turnover is concealed by near-  
 432 constant LAI. The pulses of litterfall and leaf production support compensatory leaf phenology  
 433 (Fig 1c) rather than constant leaf phenology (Fig 1b). Bars show mean values of annual amplitude  
 434 scaled for studies (n=5 sites) of lowland evergreen tropical forests where both LAI and litterfall  
 435 have been measured. Seasonal range is the annual amplitude scaled by mean value and is calculated  
 436 as the difference between the maximum dry season value and the minimum wet season value,  
 437 divided by the mean annual value (%). Error bars show standard deviation of the mean. Studies  
 438 included in this figure: Tambopata-Candamo Reserve, south-eastern Peru (Girardin et al. 2016);  
 439 Caxiuna, Floresta Nacional de Caxiuna, Pará, Brazil (Girardin et al. 2016); K83 (Doughty &  
 440 Goulden 2008) and K67 (Brando et al. 2010 and Malhado et al. 2009) are located in the Tapajós  
 441 National Forest, Pará, Brazil. Sites experience a range of mean annual precipitation values (1900  
 442 – 2572 mm).

443 This interpretation is consistent with studies asserting that tropical evergreen forests produce new  
 444 leaves during periods of high light if they are not strongly water-limited (Doughty & Goulden,  
 445 2008; Graham et al., 2003; Guan et al., 2015; M. O. Jones et al., 2014; Reich & Borchert, 1984;  
 446 Restrepo-Coupe et al., 2013; van Schaik et al., 1993; Wu et al., 2016). This continuum between  
 447 precipitation-driven and light-driven tropical evergreen forest phenological strategies is not

448 included in most TBMs, and therefore might account for some of the divergence in their GPP  
 449 projections (Restrepo-Coupe et al., 2017).



450  
 451 Figure 5: Illustration of how cryptic leaf turnover creates a phenological pattern in canopy  
 452 photosynthetic capacity. Top: Individual crowns drop old leaves and produce new leaves with  
 453 some degree of synchronization. Middle: the proportion of leaf area index belonging to previous  
 454 year's growth (old leaves) and new leaf growth (new leaves) changes through the dry season. Here  
 455 leaf phenology is difficult to detect because of compensatory inputs and outputs (see Fig 1c). Inset:

456 leaf photosynthetic capacity depends upon leaf age. Lower panel: the combination of leaf turnover  
457 and leaf ontogeny increase the canopy photosynthetic capacity, but neither total LAI nor satellite-  
458 based proxies for LAI and greenness show this same increase.

459 Equatorial Amazon sites such as K67 provide an example where resolving ambiguous  
460 phenology by testing whether leaf phenology is compensatory versus constant, and  
461 acknowledging the age-dependent physiology of leaves, is important for understanding and  
462 modeling a process, such as forest photosynthesis, at a large scale. Some plant functional types  
463 (PFTs) within TBMs allow for photosynthesis to vary with leaf age, but with a focus on  
464 temperate deciduous plants. For example, the Joint UK Land Environment Simulator (JULES)  
465 accounts for damage and senescence accumulation by reducing photosynthesis during the  
466 growing season (Clark et al., 2011), and the Ecosystem Demography model (ED2) decreases the  
467 maximum carboxylation rate of Rubisco ( $V_{\text{cmax}}$ ) in the autumn as a function of Julian day  
468 utilizing historical MODIS data (Medvigy, Wofsy, Munger, Hollinger, & Moorcroft, 2009). In  
469 these cases, time of year or ‘season’ serves as a proxy for leaf age, which may work well for  
470 some PFTs, but not for tropical evergreen broadleaf forests where the ‘evergreen’ canopy belies  
471 cyclic leaf turnover that the PFT ruleset does not include. This case study suggests that  
472 accounting for cryptic phenology is necessary for correctly detecting, attributing, and modeling  
473 the carbon exchange dynamics of tropical forests (De Weirdt et al., 2012; Y. Kim et al., 2012;  
474 Manoli, Ivanov, & Fatichi, 2018; Restrepo-Coupe et al., 2017).

475

#### 476 **4. IMPLICATIONS OF CRYPTIC PHENOLOGY FOR PREDICTION ACROSS**

#### 477 **SCALES**

478 Fine-scale processes, integrated over space and time, create large-scale exchanges of mass and  
479 energy between the biosphere and the atmosphere (Monson & Baldocchi, 2014). Here we  
480 consider some of the fine-scale processes associated with cryptic phenology that, scaled up, have

481 implications for our ability to understand, model, and predict biosphere-atmosphere interactions  
482 under climate change.

483

#### 484 *Organ scale*

485 Plant traits can show very high within-species variation due to phenology (Chavana-  
486 Bryant et al., 2017), and this variation can surpass interspecific variation for some traits (Fajardo  
487 & Siefert, 2016). Specifically, leaf development and aging is associated with changes in internal  
488 leaf structure (Lim, Kim, & Gil Nam, 2007; Niinemets et al., 2012), concentrations of secondary  
489 metabolites (Z. Liu et al., 1998; Virjamo & Julkunen-Tiitto, 2014), emissions of volatile organic  
490 compounds (Alves, Harley, Goncalves, da Silva Moura, & Jardine, 2014; Niinemets et al., 2010),  
491 and metabolic rates (Albert et al., 2018; Niinemets et al., 2012; Pantin et al., 2012). For the goal  
492 of scaling fluxes from leaves to canopies, these many physiological changes associated with leaf  
493 age suggest that distinguishing between constant leaf phenology and compensatory leaf  
494 phenology is important not only for tropical forests (as we describe in the first case study above),  
495 but for evergreen forests in general.

496 Similarly, root production is accompanied by physiological changes. There are species-  
497 specific relationships between root age and root physiology such as respiration rates and nutrient  
498 uptake capacity (Bouma et al., 2001; Fukuzawa, Dannoura, & Shibata, 2011). Existing studies  
499 that have characterized the hidden phenology of roots have shown evidence of interspecific  
500 differences in cycles of fine root production—single flushes, multiple flushes, or constant  
501 growth—that could represent strategies for responding to seasonal changes in climate or resource  
502 availability (Fukuzawa et al., 2011; McCormack et al., 2014).

503

504 *Organismal scale*

505 Natural selection would be expected to favor coordination in the timing of resource acquisition  
506 with resource storage and allocation (Sala, Woodruff, & Meinzer, 2012). Since selection acts at  
507 the level of individuals, if we want to understand the adaptive value of phenological changes, we  
508 need to understand how all plant organs function together, as a unit, through time. It is very  
509 difficult to study ‘whole’ plants in the wild, especially woody plants. Few (if any) studies have  
510 quantified the phenologies of all plant organs in wild woody plants to gain an integrated  
511 organism-level perspective on phenology (but see Hu et al., (2010) for whole-tree carbon  
512 assimilation during the growing season; see Würth, Peláez-Riedl, Wright, & Korner (2005) for  
513 seasonal variation in non-structural carbohydrate pools by plant organ; and see Doughty et al.,  
514 (2014) for an example plot-scale study of wood, fine root, and canopy phenology). Studies  
515 examining phenologies of two organs suggest that phenology is often asynchronous across  
516 organs (Abramoff & Finzi, 2015; Wagner, Rossi, Stahl, Bonal, & Hérault, 2013). Comparing  
517 phenological patterns of roots and shoots frequently reveals offsets between maximum root  
518 growth and shoot growth, and these offsets vary across biomes (Abramoff & Finzi, 2015). In  
519 tropical forests, leaf and wood production is often asynchronous (Wagner et al., 2013). The onset  
520 and/or termination of growth may also vary; roots in temperate deciduous white oak, for  
521 example, continue to elongate in winter after senescence of leaves (Teskey & Hinckley, 1981).  
522 Nonstructural carbohydrate reserves also show phenological patterns that are species-dependent  
523 (Würth et al., 2005) and affected by phenological patterns of leaves (Palacio, Maestro, &  
524 Montserratmarti, 2007). Rates of carbon use regulate carbon uptake in plants (sink-driven  
525 photosynthesis; Fatichi, Leuzinger, & Korner, 2014), so phenological changes in carbon demand  
526 should impact the timing of photosynthetic activity.

527           These findings show that capturing the patterns and drivers of hidden and ambiguous  
528 phenologies will be needed for a comprehensive understanding of how plants prioritize amongst  
529 competing uses of resources and maintain carbon balance, with implications for modeling plant  
530 resource use. In most TBMs, the temporal patterns of leaf activity (the size of the leaf pool and  
531 the rate of photosynthesis) drive temporal patterns of carbon allocation because carbon allocation  
532 to other plant organs is often modeled as a constant proportion of carbon uptake (Abramoff &  
533 Finzi, 2015; Delpierre et al., 2016; Guillemot et al., 2017). However, if different plant organs  
534 respond to different environmental drivers (Wagner et al., 2016), then models that use leaf  
535 activity to generate interannual patterns of activity in hidden organs may fail to simulate  
536 observed patterns of root or bole activity at seasonal timescales.

537           How plants prioritize their allocation, through time, to various plant organs or to storage  
538 may have consequences for plant resilience or vulnerability to extreme events, and several  
539 studies already show that plant vulnerability and/or resilience to extreme events varies due to  
540 phenological status and/or season (Craine et al., 2012; M. Huang, Wang, Keenan, & Piao, 2018).  
541 We suggest that the timing of extreme events in relation to plant phenological status may be  
542 necessary for predicting plant community responses to future climate. For example, plant  
543 tolerance to drought or cold could depend on nonstructural carbohydrates (Dietze et al., 2014;  
544 Sala et al., 2012), and nonstructural carbohydrates follow seasonal cycles that could indicate  
545 internal phenology (Richardson et al., 2013a). Tests of such hypotheses are timely, given that the  
546 frequency of extreme climate events is increasing under global climate change (Bellprat &  
547 Doblus-Reyes, 2016; Ummenhofer & Meehl, 2017).

548

549 *Community scale*

550 As climate changes, many studies have demonstrated that phenological patterns shift,  
551 impacting species interactions (CaraDonna, Iler, & Inouye, 2014; Memmott, Craze, Waser, &  
552 Price, 2007; Miller-Rushing, Hoyer, Inouye, & Post, 2010; Polgar & Primack, 2011; Rafferty,  
553 CaraDonna, & Bronstein, 2014; Yang & Rudolf, 2010). Fewer studies have probed how hidden  
554 phenologies shape species interactions, or how those interactions may be changing. To do so  
555 could reveal that phenology mediates impacts of species interactions on plant mortality,  
556 reproduction, and metabolism. For example, the timing of insect outbreaks in relation to  
557 nonstructural carbohydrate reserves (which are affected by the timing of leaf renewal) may  
558 explain interspecific differences in tolerance to defoliation (Chen, Wang, Dai, Wan, & Liu,  
559 2017). Further investigation into how species interactions affect hidden phenologies would help  
560 gain a more complete understanding of the interplay between climate change, whole plant  
561 physiology, and species interactions.

562

### 563 *Ecosystem to global scale*

564 Projections of Earth's future climate are particularly sensitive to uncertainties in the land  
565 carbon cycle (Friedlingstein et al., 2014). Improving representation of the land carbon cycle in  
566 TBMs requires understanding the drivers of phenology, and the role of phenology in mediating  
567 biosphere-atmosphere exchanges (Richardson, Keenan, et al., 2013b). Recognizing phenological  
568 rhythms at scales from plant organs to communities is prerequisite to identifying their role in  
569 large scale (ecosystem to global) cycling of carbon. For example, investigating the distribution of  
570 root ages at different times of the year could elucidate larger scale autotrophic respiration or soil  
571 resource acquisition processes (because root age affects root respiration and nutrient uptake  
572 capacity; Bouma et al., 2001). TBMs which are calibrated to match current observations, but that

573 include inaccurate relationships between drivers and vegetation responses, risk making biased  
574 predictions of forest response to future climate changes because they do not incorporate  
575 underlying biological mechanisms (De Weirdt et al., 2012; Restrepo-Coupe et al., 2017).

576

## 577 **5. RECOMMENDATIONS FOR MEASURING AND MODELING CRYPTIC**

### 578 **PHENOLOGY**

#### 579 **5.1 Recommendations for empirical research**

580 To reveal cryptic phenological patterns empirically, we need to consider the target, frequency,  
581 and methods of measurements. We recommend complementing existing studies and  
582 measurements of aboveground, clearly visible phenological changes with measurements of  
583 hidden phenological changes (Table 1). Specifically, we need more time series of development  
584 and growth of roots (e.g. Abramoff and Finzi 2015, McCormack et al 2014), and internal  
585 structures (e.g. Cuny et al. 2015), to learn when leaf phenology directly fuels the phenological  
586 patterns of other plant organs (and thus can represent them by proxy), and when it does not.  
587 Building upon studies examining synchrony in phenology of multiple plant organs (Bazié et al.,  
588 2017; Delpierre et al., 2016; Michelot, Simard, Rathgeber, Dufrene, & Damesin, 2012; Omondi,  
589 Odee, Ongamo, Kanya, & Khasa, 2016; Perrin, Rossi, & Isabel, 2017; Wagner et al., 2013),  
590 whole-plant phenology studies in which all plant organs and their associated processes  
591 (acquisition and allocation of carbon, water, and nutrients) are continuously monitored in the  
592 same individual plants across seasons could elucidate the relationship between the phenology of  
593 plant organs with each other, and with climate, and test the representation of phenology for  
594 various PFTs.

595           Revealing cryptic phenological patterns will require more studies explicitly testing  
596 whether compensatory processes (Fig. 1c) mistaken for constancy (Fig. 1b) mislead our  
597 interpretation of mass, area, or volume time series. To this end, sampling schemes need to go  
598 beyond measuring mass, area or volume of plant organs or “pools” (in aggregate) to also  
599 measure rates of inputs and outputs to and from organs/pools across time. (Since mass-balance  
600 equations have three terms—inputs, outputs, and the accumulated pool—at least two must be  
601 measured to obtain a single solution). For example, litterfall time series should be collected to  
602 correspond with total leaf area time series. To examine the metabolic consequences of constant  
603 versus compensating phenology, we need more (1) measurements of plant organ activity as  
604 organs develop and age, and (2) experiments manipulating phenological status to test the  
605 interaction between phenology and physiology (including photosynthesis and respiration) under  
606 various treatments (e.g. drought, temperature, and herbivory). When a measured variable (e.g.  
607 mass or volume) is the sum of multiple component variables (Fig 1a) then those components  
608 should be characterized (if possible) in tests for scenarios when the time series of the measured  
609 variable is not aligned with that of the component variable of interest. Fourier analysis is a  
610 promising tool for decomposing phenological cycles (Bush et al., 2016), and should be explored  
611 for revealing phenology that is otherwise ambiguous.

612           Phenological events can happen quickly and vary across landscapes. Fine temporal and  
613 spatial resolution will capture patterns that might otherwise be missed (e.g. Smith et al. 2019).  
614 How we measure phenological patterns has moved beyond plant-level measurements to  
615 landscape measurements as technology has evolved, and we need to continue expanding our  
616 capacity for detecting plant phenological activity at multiple spatial scales (e.g. leaves to  
617 canopies to landscapes). Remote sensing technologies offer valuable tools for gathering

618 phenological data on large spatial scales. Chlorophyll fluorescence remote sensing products  
619 promise to test the physiological interpretation of ‘greenness’ from the more traditional MODIS  
620 products (Guan et al., 2015; Lee et al., 2013; Porcar-Castell et al., 2014). Continuous or frequent  
621 high resolution near-surface remote sensing instrumentation such as phenocams (Klosterman et  
622 al., 2014; Lopes et al., 2016; Wu et al., 2016) and lidar (Calders et al., 2015) offer finer spatial  
623 resolution data to complement and potentially validate satellite-based phenology-related  
624 products.

625         Although satellite-derived products are valuable tool for phenology (e.g. Guan et al  
626 2015), some phenological patterns remain cryptic when relying on remote sensing tools.  
627 Reflectance-based indices from satellites reveal more about the phenological status of upper  
628 canopy leaves and shoots than about the hidden phenological activity of roots, boles, and internal  
629 plant processes. Further development of remote sensing tools may help reveal hidden  
630 phenologies; for example, lidar can be used to estimate LAI at all canopy heights, helping infer  
631 leaf phenological patterns for deeper canopy layers that are hidden from other sensors (Tang &  
632 Dubayah, 2017). We urge more tests to evaluate when remote sensing signals do, and do not, link  
633 to phenology, including time series of comparisons between remote sensing signals and plant-  
634 level measurements (e.g. changes in leaf production or woody biomass). In addition, the  
635 development of high-throughput methods for evaluating gene expression (Kris et al., 2007),  
636 together with the growing databases of annotated genomes, offer the opportunity to complement  
637 aboveground measurements with information about regulation of internal or below-ground  
638 activities.

639

## 640 **5.2 Recommendations for model development**

641 In TBMs, plant structures (e.g. leaves) are produced or shed, and processes are switched ‘on’ or  
642 ‘off’, based on rule sets about temperature, moisture, and photoperiod, or (in about a third of  
643 TBMs), are prescribed based on remotely sensed indices and other derived products instead of  
644 being simulated internally (Fisher et al., 2014; Huntzinger et al., 2012). In either case, the TBM  
645 representation of phenological processes relies heavily on observations that are readily collected  
646 at large scales, such as climate data and satellite-based remote sensing products. We need to  
647 determine when this reliance on apparent phenology limits our ability to make robust long-term  
648 predictions of terrestrial carbon, water, and energy budgets or future boundary shifts of biomes.

649 A process or parameter in a model is important, in terms of our predictive ability, if it  
650 causes large changes in a response that we want to predict (high sensitivity), and/or if it is highly  
651 uncertain (Dietze, 2017). For TBMs, we need more sensitivity analyses that evaluate the impact  
652 of including or excluding potential phenological schemes, and uncertainty assessments that  
653 quantify sources of uncertainty (e.g. Migliavacca et al., 2012). Specific phenological dynamics  
654 ripe for possible implementation in TBMs include asynchronous allocation to various plant  
655 organs (e.g. through prioritization schemes or time lags), environmental controls over carbon  
656 allocation (Guillemot et al., 2017), and plant organ age-dependency of metabolic capacity (e.g.  
657 photosynthetic capacity as a function of leaf age and root respiration as a function of root age;  
658 (Albert et al., 2018; De Weirdt et al., 2012; Fukuzawa et al., 2011). By examining the sensitivity  
659 of modelled ecosystem-scale fluxes to such processes, modelers can strike a balance between  
660 over-parametrizing versus excluding important processes in TBM models. Knowledge of which  
661 phenological states, processes, and parameters within models show high sensitivity or  
662 uncertainty can also help guide empirical research priorities.

663 Evaluations of uncertainty and sensitivity require first having model formulations of  
664 phenology. As we have argued, study efforts are not uniform, and phenological patterns may be  
665 cryptic such that they can only be resolved with multiple measurements (e.g. inputs and outputs  
666 or multiple variables). In these cases, it may be difficult to find enough information to develop  
667 phenology schemes. Model-data comparisons, with observational data coming from multiple  
668 independent sources (and multiple organs) at multiple scales (e.g. eddy covariance time series,  
669 and measurements of allocation in individuals) should help determine if an important  
670 phenological process could be wholly missing from models. Joint model and empirical efforts  
671 can then identify, characterize, model, and evaluate the importance of the excluded phenological  
672 processes.

673 Finally, we emphasize the value of drawing upon empirical and theoretical ecology,  
674 evolution, and physiology for the development and refinement of phenological models. In  
675 systems where the temporal dynamics of plant acquisition and allocation have been shown to be  
676 under selection to increase fitness within climatic and biological constraints, optimization models  
677 may be useful (e.g. Caldararu, Purves, & Palmer, 2014; Kikuzawa, 1991; 1996), but they should  
678 be expanded to include multiple resources (e.g. moisture and nutrient optimization in addition to  
679 carbon), and trade-offs between multiple purposes, such as growth and reproduction (Iwasa,  
680 2000). However, it is also important to recognize that life history imposes temporal structure  
681 relevant to modelling at the seasonal time scale, such as timelines for recruitment, maturation,  
682 and mortality in annual plants, or timelines for development of the photosynthetic apparatus in  
683 new leaves with different lifespans. Thus, a valuable challenge will be to formalize demographic  
684 and physiological timelines in models and test their impact on model sensitivity and uncertainty.  
685

686 **6. CONCLUSION**

687 A growing body of research shows that capturing cryptic phenologies is required for a complete  
688 picture of seasonal resource allocation and acquisition strategies, constraints, and consequences  
689 across many scales. Understanding the full scope of cyclic and recurrent biological events in  
690 plants is critical for advancing our understanding of plant ecology and evolution, and for  
691 predicting responses and feedbacks to climate change. We call for further recognition and  
692 exploration of cryptic phenologies—including compensatory processes, non-structural  
693 carbohydrates dynamics, wood formation, and root production —through new technologies,  
694 TBM development, and time series of intensive plant-scale measurements.

695

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716

## 717 REFERENCES

- 718 Abramoff, R. Z., & Finzi, A. C. (2015). Are above- and below-ground phenology in sync? *New*  
719 *Phytologist*, 205, 1054–1061. <https://doi.org/10.1111/nph.13111>
- 720 Albert, L. P., Wu, J., Prohaska, N., de Camargo, P. B., Huxman, T. E., Tribuzy, E. S., et al.  
721 (2018). Age-dependent leaf physiology and consequences for crown-scale carbon uptake  
722 during the dry season in an Amazon evergreen forest. *New Phytologist*, 219(3), 870–884.  
723 <https://doi.org/10.1111/nph.15056>
- 724 Alves, E. G., Harley, P., Goncalves, J. F. de C., da Silva Moura, C. E., & Jardine, K. (2014).  
725 Effects of light and temperature on isoprene emission at different leaf developmental stages  
726 of *Eschweilera coriacea* in central Amazon. *Acta Amazonica*, 44(1), 9–18.
- 727 Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L.  
728 (2013). Heat freezes niche evolution. *Ecology Letters*, 16(9), 1206–1219.  
729 <https://doi.org/10.1111/ele.12155>
- 730 Arend, M., & Fromm, J. (2007). Seasonal change in the drought response of wood cell  
731 development in poplar. *Tree Physiology*, 27(7), 985–992.

732 Asner, G. P. (2001). Cloud cover in Landsat observations of the Brazilian Amazon. *International*  
733 *Journal of Remote Sensing*, 22(18), 3855–3862.  
734 <https://doi.org/10.1080/01431160010006926>

735 Babst, F., Alexander, M. R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., et al. (2014). A tree-  
736 ring perspective on the terrestrial carbon cycle. *Oecologia*, 176(2), 307–322.  
737 <https://doi.org/10.1007/s00442-014-3031-6>

738 Badeck, F.-W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., & Sitch, S.  
739 (2004). Responses of spring phenology to climate change. *The New Phytologist*, 162(2),  
740 295–309. <https://doi.org/10.1111/j.1469-8137.2004.01059.x>

741 Battipaglia, G., De Micco, V., Brand, W. A., Linke, P., Aronne, G., Saurer, M., & Cherubini, P.  
742 (2010). Variations of vessel diameter and  $\delta^{13}\text{C}$  in false rings of *Arbutus unedo* L. reflect  
743 different environmental conditions. *New Phytologist*, 188(4), 1099–1112.  
744 <https://doi.org/10.1111/j.1469-8137.2010.03443.x>

745 Bauer, M. C., Meyer, S. E., & Allen, P. S. (1998). A simulation model to predict seed dormancy  
746 loss in the field for *Bromus tectorum* L. *Journal of Experimental Botany*, 49(324), 1235–  
747 1244. <https://doi.org/10.1093/jexbot/49.324.1235>

748 Bazié, P., Ky-Dembele, C., Jourdan, C., Roupsard, O., Zombré, G., & Bayala, J. (2017).  
749 Synchrony in the phenologies of fine roots and leaves of *Vitellaria paradoxa* in different land  
750 uses of Burkina Faso. *Agroforestry Systems*, 93(2), 449–460. [https://doi.org/10.1007/s10457-](https://doi.org/10.1007/s10457-017-0135-0)  
751 [017-0135-0](https://doi.org/10.1007/s10457-017-0135-0)

752 Bellprat, O., & Doblas-Reyes, F. (2016). Attribution of extreme weather and climate events  
753 overestimated by unreliable climate simulations. *Geophysical Research Letters*, 43(5), 2158–  
754 2164. <https://doi.org/10.1002/2015GL067189>

755 Bennett, A. F., & Lenski, R. E. (2007). An experimental test of evolutionary trade-offs during  
756 temperature adaptation. *Pnas*, *104*(Supplement 1), 8649–8654.  
757 <https://doi.org/10.1073/pnas.0702117104>

758 Bouma, T. J., Yanai, R. D., Elkin, A. D., Hartmond, U., Flores-Alva, D. E., & Eissenstat, D. M.  
759 (2001). Estimating age-dependent costs and benefits of roots with contrasting life span:  
760 comparing apples and oranges. *New Phytologist*, *150*(3), 685–695.

761 Buitenwerf, R., Rose, L., & Higgins, S. I. (2015). Three decades of multi-dimensional change in  
762 global leaf phenology. *Nature Climate Change*, *5*(4), 364–368.  
763 <https://doi.org/10.1038/nclimate2533>

764 Bush, E. R., Abernethy, K. A., Jeffery, K., Tutin, C., White, L., Dimoto, E., et al. (2016). Fourier  
765 analysis to detect phenological cycles using long-term tropical field data and simulations.  
766 *Methods in Ecology and Evolution*, *8*(5), 530–540. <https://doi.org/10.1111/2041-210X.12704>

767 Caldararu, S., Purves, D. W., & Palmer, P. I. (2014). Phenology as a strategy for carbon  
768 optimality: a global model. *Biogeosciences*, *11*(3), 763–778. [https://doi.org/10.5194/bg-11-](https://doi.org/10.5194/bg-11-763-2014)  
769 [763-2014](https://doi.org/10.5194/bg-11-763-2014)

770 Calders, K., Schenkels, T., Bartholomeus, H., Armston, J., Verbesselt, J., & Herold, M. (2015).  
771 Monitoring spring phenology with high temporal resolution terrestrial LiDAR  
772 measurements. *Agricultural and Forest Meteorology*, *203*, 158–168.  
773 <https://doi.org/10.1016/j.agrformet.2015.01.009>

774 CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a  
775 subalpine plant community. *Proceedings of the National Academy of Sciences*, *111*(13),  
776 4916–4921. <https://doi.org/10.1073/pnas.1323073111>

777 Cardoso, D., Särkinen, T., Alexander, S., Amorim, A. M., Bittrich, V., Celis, M., et al. (2017).  
778 Amazon plant diversity revealed by a taxonomically verified species list. *Pnas*, *114*(40),  
779 10695–10700. <https://doi.org/10.1073/pnas.1706756114>

780 Chaffey, N. (1999). Cambium: old challenges–new opportunities. *Trees-Structure and Function*,  
781 *13*, 138–151.

782 Chavana-Bryant, C., Malhi, Y., Wu, J., Asner, G. P., Anastasiou, A., Enquist, B. J., et al. (2017).  
783 Leaf aging of Amazonian canopy trees as revealed by spectral and physiochemical  
784 measurements. *The New Phytologist*, *214*(3), 1049–1063. <https://doi.org/10.1111/nph.13853>

785 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009).  
786 Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366.  
787 <https://doi.org/10.1111/j.1461-0248.2009.01285.x>

788 Chave, J., Réjou-Méchain, M., Burquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., et  
789 al. (2014). Improved allometric models to estimate the aboveground biomass of tropical  
790 trees. *Global Change Biology*, *20*(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>

791 Chen, Z., Wang, L., Dai, Y., Wan, X., & Liu, S. (2017). Phenology-dependent variation in the  
792 non-structural carbohydrates of broadleaf evergreen species plays an important role in  
793 determining tolerance to defoliation (or herbivory). *Nature Publishing Group*, 1–11.  
794 <https://doi.org/10.1038/s41598-017-09757-2>

795 Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H. S., Suresh, H. S., & Sukumar, R. (2015).  
796 Forest Ecology and Management. *Forest Ecology and Management*, *336*(C), 129–136.  
797 <https://doi.org/10.1016/j.foreco.2014.10.007>

798 Chojnacky, D. C., Heath, L. S., & Jenkins, J. C. (2014). Updated generalized biomass equations  
799 for North American tree species. *Forestry*, 87(1), 129–151.  
800 <https://doi.org/10.1093/forestry/cpt053>

801 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of*  
802 *the Royal Society B: Biological Sciences*, 365(1555), 3149–3160.  
803 <https://doi.org/10.1098/rstb.2010.0142>

804 Churkina, G., Schimel, D., Braswell, B. H., & Xiao, X. (2005). Spatial analysis of growing  
805 season length control over net ecosystem exchange. *Global Change ...*, 11, 1777–1787.  
806 <https://doi.org/10.1111/j.1365-2486.2005.01012.x>

807 Clark, D. B., & Kellner, J. R. (2012). Tropical forest biomass estimation and the fallacy of  
808 misplaced concreteness. *Journal of Vegetation Science*, 23(6), 1191–1196.  
809 <https://doi.org/10.1111/j.1654-1103.2012.01471.x>

810 Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., et al. (2011). The  
811 Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes  
812 and vegetation dynamics. *Geoscientific Model Development*, 4(3), 701–722.  
813 <https://doi.org/10.5194/gmd-4-701-2011-supplement>

814 Cleland, E., Chuine, I., Menzel, A., Mooney, H., & Schwartz, M. (2007). Shifting plant  
815 phenology in response to global change. *Trends in Ecology & Evolution*, 22(7), 357–365.  
816 <https://doi.org/10.1016/j.tree.2007.04.003>

817 Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A.  
818 (2012). Timing of climate variability and grassland productivity. *Proceedings of the*  
819 *National Academy of Sciences*, 109(9), 3401–3405. <https://doi.org/10.1073/pnas.1118438109>

820 Cuny, H. E., Rathgeber, C. B. K., Frank, D., Fonti, P., Mäkinen, H., Prislán, P., et al. (2015).  
821 Woody biomass production lags stem-girth increase by over one month in coniferous forests,  
822 1–6. <https://doi.org/10.1038/nplants.2015.160>

823 De Weirdt, M., Verbeeck, H., Maignan, F., Peylin, P., Poulter, B., Bonal, D., et al. (2012).  
824 Seasonal leaf dynamics for tropical evergreen forests in a process-based global ecosystem  
825 model. *Geoscientific Model Development*, 5(5), 1091–1108. [https://doi.org/10.5194/gmd-5-](https://doi.org/10.5194/gmd-5-1091-2012)  
826 1091-2012

827 Delpierre, N., Berveiller, D., Granda, E., & Dufrene, E. (2015). Wood phenology, not carbon  
828 input, controls the interannual variability of wood growth in a temperate oak forest. *New*  
829 *Phytologist*, 210(2), 459–470. <https://doi.org/10.1111/nph.13771>

830 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., & Rathgeber, C.  
831 B. K. (2016). Temperate and boreal forest tree phenology: from organ-scale processes to  
832 terrestrial ecosystem models, 73(1), 5–25. <https://doi.org/10.1007/s13595-015-0477-6>

833 Diamond, S. E., Frame, A. M., Martin, R. A., & Buckley, L. B. (2011). Species' traits predict  
834 phenological responses to climate change in butterflies. *Ecology*, 92(5), 1005–1012.  
835 <https://doi.org/10.1890/10-1594.1>

836 Dietze, M. C. (2017). Prediction in ecology: a first-principles framework. *Ecological*  
837 *Applications*, 27(7), 2048–2060. <https://doi.org/10.1002/eap.1589>

838 Dietze, M. C., Sala, A., Carbone, M. S., Czimeczik, C. I., Mantooh, J. A., Richardson, A. D., &  
839 Vargas, R. (2014). Nonstructural Carbon in Woody Plants. *Annual Review of Plant Biology*,  
840 65(1), 667–687. <https://doi.org/10.1146/annurev-arplant-050213-040054>

841 Doughty, C. E., & Goulden, M. L. (2008). Seasonal patterns of tropical forest leaf area index and  
842 CO<sub>2</sub> exchange. *Journal of Geophysical Research*, *113*(October), G00B06.  
843 <https://doi.org/10.1029/2007JG000590>

844 Doughty, C. E., Malhi, Y., Araujo-Murakami, A., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo,  
845 L., et al. (2014). Allocation trade-offs dominate the response of tropical forest growth to  
846 seasonal and interannual drought. *Ecology*, *95*(8), 2192–2201.

847 Escudero, A., & Del Arco, J. M. (1987). Ecological significance of the phenology of leaf  
848 abscission. *Oikos*, *49*(1), 11–14.

849 Fajardo, A., & Siefert, A. (2016). Phenological variation of leaf functional traits within species.  
850 *Oecologia*, *180*(4), 951–959. <https://doi.org/10.1007/s00442-016-3545-1>

851 Fatichi, S., Leuzinger, S., & Korner, C. (2014). Moving beyond photosynthesis: from carbon  
852 source to sink-driven vegetation modeling. *The New Phytologist*, *201*(4), 1086–1095.  
853 <https://doi.org/10.1111/nph.12614>

854 Fisher, J. B., Huntzinger, D. N., Schwalm, C. R., & Sitch, S. (2014). Modeling the Terrestrial  
855 Biosphere. *Annual Review of Environment and Resources*, *39*(1), 91–123.  
856 <https://doi.org/10.1146/annurev-environ-012913-093456>

857 Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of  
858 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B:*  
859 *Biological Sciences*, *365*(1555), 3101–3112. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2008.01367.x)  
860 [2656.2008.01367.x](https://doi.org/10.1111/j.1365-2656.2008.01367.x)

861 Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., &  
862 Knutti, R. (2014). Uncertainties in CMIP5 Climate Projections due to Carbon Cycle  
863 Feedbacks. *Journal of Climate*, *27*(2), 511–526. <https://doi.org/10.1175/JCLI-D-12-00579.1>

864 Fukuzawa, K., Dannoura, M., & Shibata, H. (2011). Fine Root Dynamics and Root Respiration.  
865 In S. Mancuso (Ed.), *Measuring Roots* (pp. 291–302). Berlin, Heidelberg: Springer Berlin  
866 Heidelberg. [https://doi.org/10.1007/978-3-642-22067-8\\_15](https://doi.org/10.1007/978-3-642-22067-8_15)

867 Gaudinski, J. B., Torn, M. S., Riley, W. J., Dawson, T. E., Joslin, J. D., & Majdi, H. (2010).  
868 Measuring and modeling the spectrum of fine-root turnover times in three forests using  
869 isotopes, minirhizotrons, and the Radix model. *Global Biogeochemical Cycles*, 24(3), n/a–  
870 n/a. <https://doi.org/10.1029/2009GB003649>

871 Getz, W. M., Marshall, C. R., Carlson, C. J., Giuggioli, L., Ryan, S. J., Romañach, S. S., et al.  
872 (2017). Making ecological models adequate. *Ecology Letters*, 21(2), 153–166.  
873 <https://doi.org/10.1111/ele.12893>

874 Girardin, C.A., Malhi, Y., Doughty, C. E., Metcalfe, D.B., Meir, P., del Aguila-Pasquel, J.,  
875 Araujo-Murakami, A., da Costa, A.C., Silva-Espejo, J.E., Farfan Amezcuita, F. and  
876 Rowland, L. (2016). Seasonal trends of Amazonian rainforest phenology, net primary  
877 productivity, and carbon allocation. *Global Biogeochemical Cycles*, 30, 700–715.  
878 [https://doi.org/10.1002/\(ISSN\)1944-9224](https://doi.org/10.1002/(ISSN)1944-9224)

879 Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover  
880 limits net CO<sub>2</sub> uptake and growth of a rainforest tree during tropical rainy seasons.  
881 *Proceedings of the National Academy of Sciences*, 100(2), 572–576.  
882 <https://doi.org/10.1073/pnas.0133045100>

883 Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., et al. (2015). Photosynthetic  
884 seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*, 8(4),  
885 284–289. <https://doi.org/10.1038/ngeo2382>

886 Guillemot, J., François, C., Hmimina, G., Dufrene, E., Martin-StPaul, N. K., Soudani, K., et al.  
887 (2017). Environmental control of carbon allocation matters for modelling forest growth. *New*  
888 *Phytologist*, 214(1), 180–193. <https://doi.org/10.1111/nph.14320>

889 Guo, J. S., & Ogle, K. (2018). Antecedent soil water content and vapor pressure deficit  
890 interactively control water potential in *Larrea tridentata*. *New Phytologist*, 221(1), 218–232.  
891 <https://doi.org/10.1111/nph.15374>

892 Hardegree, S. P. (2006). Predicting Germination Response to Temperature. I. Cardinal-  
893 temperature Models and Subpopulation-specific Regression. *Annals of Botany*, 97(6), 1115–  
894 1125. <https://doi.org/10.1093/aob/mcl071>

895 Hu, J., Moore, D. J. P., Riveros-Iregui, D. A., Burns, S. P., & Monson, R. K. (2010.). Modeling  
896 whole-tree carbon assimilation rate using observed transpiration rates and needle sugar  
897 carbon isotope ratios. *The New Phytologist*, 185(4), 1000–1015.  
898 <https://doi.org/10.1111/j.1469-8137.2009.03154.x>

899 Huang, M., Wang, X., Keenan, T. F., & Piao, S. (2018). Drought timing influences the legacy of  
900 tree growth recovery. *Global Change Biology*, 37, 418–414.  
901 <https://doi.org/10.1111/gcb.14294>

902 Huang, Z., Liu, S., Bradford, K. J., Huxman, T. E., & Venable, D. L. (2016). The contribution of  
903 germination functional traits to population dynamics of a desert plant community. *Ecology*,  
904 97(1), 250–261.

905 Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyyra, L. R., et al.  
906 (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research*  
907 *Letters*, 33(6), L06405.

908 Huntzinger, D. N., Post, W. M., Wei, Y., Michalak, A. M., West, T. O., Jacobson, A. R., et al.  
909 (2012). Ecological Modelling. *Ecological Modelling*, 232, 144–157.  
910 <https://doi.org/10.1016/j.ecolmodel.2012.02.004>

911 Iwasa, Y. (2000). Dynamic optimization of plant growth. *Evolutionary Ecology Research*, 2,  
912 437–455.

913 Jones, M. O., Kimball, J. S., & Nemani, R. R. (2014). Asynchronous Amazon forest canopy  
914 phenology indicates adaptation to both water and light availability. *Environmental Research*  
915 *Letters*, 9(12), 1–10. <https://doi.org/10.1088/1748-9326/9/12/124021>

916 Ju, W., Chen, J. M., Black, T. A., Barr, A. G., Liu, J., & Chen, B. (2006). Modelling multi-year  
917 coupled carbon and water fluxes in a boreal aspen forest. *Agricultural and Forest*  
918 *Meteorology*, 140(1-4), 136–151. <https://doi.org/10.1016/j.agrformet.2006.08.008>

919 Kikuzawa, K. (1991). A cost-benefit analysis of leaf habit and leaf longevity of trees and their  
920 geographical pattern. *American Naturalist*, 138(5), 1250–1263.

921 Kikuzawa, K. (1996). Geographical distribution of leaf life span and species diversity of trees  
922 simulated by a leaf-longevity model. *Vegetatio*, 122, 61–67.

923 Kim, Y., Knox, R. G., Longo, M., Medvigy, D., Hutyyra, L. R., Pyle, E. H., et al. (2012).  
924 Seasonal carbon dynamics and water fluxes in an Amazon rainforest. *Global Change*  
925 *Biology*, 18(4), 1322–1334. <https://doi.org/10.1111/j.1365-2486.2011.02629.x>

926 Klosterman, S. T., Hufkens, K., Gray, J. M., Melaas, E., Sonnentag, O., Lavine, I., et al. (2014).  
927 Evaluating remote sensing of deciduous forest phenology at multiple spatial scales using  
928 PhenoCam imagery. *Biogeosciences*, 11(16), 4305–4320. [https://doi.org/10.5194/bg-11-](https://doi.org/10.5194/bg-11-4305-2014)  
929 4305-2014

930 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., et al.  
931 (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere  
932 system. *Global Biogeochemical Cycles*, *19*(1), GB1015.  
933 <https://doi.org/10.1029/2003GB002199>

934 Kris, R. M., Felder, S., Deyholos, M., Lambert, G. M., Hinton, J., Botros, I., et al. (2007). High-  
935 throughput, high-sensitivity analysis of gene expression in Arabidopsis. *Plant Physiology*,  
936 *144*(3), 1256–1266. <https://doi.org/10.1104/pp.107.098681>

937 Le Quéré, C., Moriarty, R., Andrew, R. M., Peters, G. P., Ciais, P., Friedlingstein, P., et al.  
938 (2015). Global carbon budget 2014. *Earth System Science Data*, *7*(1), 47–85.  
939 <https://doi.org/10.5194/essd-7-47-2015>

940 Lee, J. E., Frankenberg, C., van der Tol, C., Berry, J. A., Guanter, L., Boyce, C. K., et al. (2013).  
941 Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll  
942 fluorescence. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1761),  
943 20130171–20130171. <https://doi.org/10.1126/science.1184984>

944 Leopold, A., & Jones, S. E. (1947). A phenological record for Sauk and Dane Counties,  
945 Wisconsin, 1935-1945. *Ecological Monographs*, *17*(1), 81–122.

946 Lieth, H. (1974). Phenology and Seasonality Modeling. Springer Science & Business Media.  
947 <https://doi.org/10.1007/978-3-642-51863-8>

948 Lim, P. O., Kim, H. J., & Gil Nam, H. (2007). Leaf Senescence. *Annual Review of Plant Biology*,  
949 *58*(1), 115–136. <https://doi.org/10.1146/annurev.arplant.57.032905.105316>

950 Liu, Z., Carpenter, S. B., Bourgeois, W. J., Yu, Y., Constantin, R. J., Falcon, M., & Adams, J.  
951 (1998). Variations in the secondary metabolite camptothecin in relation to tissue age and  
952 season in *Camptotheca acuminata*. *Biological Journal of the Linnean Society*, *18*, 265–270.

953 Lopes, A. P., Nelson, B. W., Wu, J., de Alencastro Graça, P. M. L., Tavares, J. V., Prohaska, N.,  
954 et al. (2016). Leaf flush drives dry season green-up of the Central Amazon. *Remote Sensing*  
955 *of Environment, 182*, 90–98. <https://doi.org/10.1016/j.rse.2016.05.009>

956 Manoli, G., Ivanov, V. Y., & Fatichi, S. (2018). Dry-Season Greening and Water Stress in  
957 Amazonia: The Role of Modeling Leaf Phenology. *Journal of Geophysical Research:*  
958 *Biogeosciences, 123*(6), 1909–1926. <https://doi.org/10.1029/2017JG004282>

959 McCormack, M. L., Adams, T. S., Smithwick, E. A. H., & Eissenstat, D. M. (2014). Variability  
960 in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology*,  
961 *95*(8), 2224–2235.

962 McMahon, S. M., & Parker, G. G. (2015). A general model of intra-annual tree growth using  
963 dendrometer bands. *Ecology and Evolution, 5*(2), 243–254.  
964 <https://doi.org/10.1002/ece3.1117>

965 McMahon, S. M., Parker, G. G., & Miller, D. R. (2010). Evidence for a recent increase in forest  
966 growth. *Proceedings of the National Academy of Sciences, 107*(8), 3611–3615.  
967 <https://doi.org/10.1073/pnas.0912376107>

968 Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y., & Moorcroft, P. R. (2009).  
969 Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem  
970 Demography model version 2. *Journal of Geophysical Research, 114*(G1), G01002.  
971 <https://doi.org/10.1029/2008JG000812>

972 Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the  
973 disruption of plant-pollinator interactions. *Ecology Letters, 10*(8), 710–717.  
974 <https://doi.org/10.1111/j.1461-0248.2007.01061.x>

975 Michelot, A., Simard, S., Rathgeber, C., Dufrene, E., & Damesin, C. (2012). Comparing the  
976 intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea*  
977 and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics.  
978 *Tree Physiology*, 32(8), 1033–1045. <https://doi.org/10.1093/treephys/tps052>

979 Migliavacca, M., Reichstein, M., Richardson, A. D., Mahecha, M. D., Cremonese, E., Delpierre,  
980 N., et al. (2015). Influence of physiological phenology on the seasonal pattern of ecosystem  
981 respiration in deciduous forests. *Global Change Biology*, 21(1), 363–376.  
982 <https://doi.org/10.1111/gcb.12671>

983 Migliavacca, M., Sonnentag, O., Keenan, T. F., Cescatti, A., O'Keefe, J., & Richardson, A. D.  
984 (2012). On the uncertainty of phenological responses to climate change, and implications for  
985 a terrestrial biosphere model. *Biogeosciences*, 9(6), 2063–2083. [https://doi.org/10.5194/bg-](https://doi.org/10.5194/bg-9-2063-2012)  
986 [9-2063-2012](https://doi.org/10.5194/bg-9-2063-2012)

987 Miller-Rushing, A. J., Hoyer, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological  
988 mismatches on demography. *Philosophical Transactions of the Royal Society of London.*  
989 *Series B, Biological Sciences*, 365(1555), 3177–3186. <https://doi.org/10.1098/rstb.2010.0148>

990 Monson, R. K., & Baldocchi, D. D. (2014). *Terrestrial Biosphere-Atmosphere Fluxes*.  
991 Cambridge: Cambridge University Press.

992 Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., Cook, B. D., et al. (2014).  
993 Amazon forests maintain consistent canopy structure and greenness during the dry season.  
994 *Nature*, 506(7487), 221–224. <https://doi.org/10.1038/nature13006>

995 Mullen, R. B., & Schmidt, S. K. (1993). Mycorrhizal infection, phosphorus uptake, and  
996 phenology in *Ranunculus adoneus*: implications for

997 the functioning of mycorrhizae in alpine systems. *Oecologia*, 94(2), 229–234.  
998 <https://doi.org/10.1007/BF00341321>

999 Munger, J. W. (n.d.). (1991-) AmeriFlux US-Ha1 Harvard Forest EMS Tower (HFR1).  
1000 <https://doi.org/10.17190/AMF/1246059>

1001 Munger, W., & Wofsy, S. C. (2018). Biomass Inventories at Harvard Forest EMS Tower since  
1002 1993. <https://doi.org/10.6073/pasta/37ff12d47894a73ddd9d86c1225e2dc8>

1003 Murali, K. S., & Sukumar, R. (1993). Leaf flushing phenology and herbivory in a tropical dry  
1004 deciduous forest, southern India. *Oecologia*.

1005 Newell, E., Mulkey, S., & Wright, S. (2002). Seasonal patterns of carbohydrate storage in four  
1006 tropical tree species. *Oecologia*, 131(3), 333–342.

1007 Niinemets, U., Arneth, A., Kuhn, U., Monson, R. K., Penuelas, J., & Staudt, M. (2010). The  
1008 emission factor of volatile isoprenoids: stress, acclimation, and developmental responses.  
1009 *Biogeosciences*, 7(7), 2203–2223. <https://doi.org/10.5194/bg-7-2203-2010>

1010 Niinemets, U., García-Plazaola, J. I., & Tosens, T. (2012). Photosynthesis during leaf  
1011 development and ageing. In *Terrestrial Photosynthesis in a Changing Environment*.  
1012 Cambridge University Press.

1013 Noormets, A. (2009). Phenology of Ecosystem Processes. Springer Science & Business Media.

1014 Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., et al.  
1015 (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*,  
1016 18(3), 221–235. <https://doi.org/10.1111/ele.12399>

1017 Omondi, S. F., Odee, D. W., Ongamo, G. O., Kanya, J. I., & Khasa, D. P. (2016). Synchrony in  
1018 Leafing, Flowering, and Fruiting Phenology of *Senegalia senegal* within Lake Baringo

1019 Woodland, Kenya: Implication for Conservation and Tree Improvement. *International*  
1020 *Journal of Forestry Research*, 2016(4), 1–11. <https://doi.org/10.1155/2016/6904834>

1021 Palacio, S., Maestro, M., & Montserratmarti, G. (2007). Seasonal dynamics of non-structural  
1022 carbohydrates in two species of mediterranean sub-shrubs with different leaf phenology.  
1023 *Environmental and Experimental Botany*, 59(1), 34–42.  
1024 <https://doi.org/10.1016/j.envexpbot.2005.10.003>

1025 Pantin, F., Simonneau, T., & Muller, B. (2012). Coming of leaf age: control of growth by  
1026 hydraulics and metabolics during leaf ontogeny. *New Phytologist*, 196(2), 349–366.  
1027 <https://doi.org/10.1111/j.1469-8137.2012.04273.x>

1028 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts  
1029 across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>

1030 Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., et al. (2011).  
1031 Predicting phenology by integrating ecology, evolution and climate science. *Global Change*  
1032 *Biology*, 17(12), 3633–3643. <https://doi.org/10.1111/j.1365-2486.2011.02515.x>

1033 Perrin, M., Rossi, S., & Isabel, N. (2017). Synchronisms between bud and cambium phenology  
1034 in black spruce: early-flushing provenances exhibit early xylem formation. *Tree Physiology*,  
1035 37(5), 593–603. <https://doi.org/10.1093/treephys/tpx019>

1036 phenology, n. : Oxford English Dictionary. (2005). phenology, n. : Oxford English Dictionary  
1037 (Third). OED Online. Retrieved from <http://www.oed.com>

1038 Plomion, C., Leprovost, G., & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*,  
1039 127(4), 1513–1523. <https://doi.org/10.1104/pp.010816>

1040 Polgar, C. A., & Primack, R. B. (2011). Leaf-out phenology of temperate woody plants: from  
1041 trees to ecosystems. *New Phytologist*, 191(4), 926–941.

1042 Porcar-Castell, A., Tyystjarvi, E., Atherton, J., van der Tol, C., Flexas, J., Pfundel, E. E., et al.  
1043 (2014). Linking chlorophyll a fluorescence to photosynthesis for remote sensing  
1044 applications: mechanisms and challenges. *Journal of Experimental Botany*, 65(15), 4065–  
1045 4095. <https://doi.org/10.1093/jxb/eru191>

1046 Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a  
1047 changing climate. *Journal of Experimental Botany*, 67(12), 3617–3628.  
1048 <https://doi.org/10.1093/jxb/erw062>

1049 Rafferty, N. E., CaraDonna, P. J., & Bronstein, J. L. (2014). Phenological shifts and the fate of  
1050 mutualisms. *Oikos*, 124(1), 14–21. <https://doi.org/10.1111/oik.01523>

1051 Rathcke, B., & Lacey, E. P. (1985). Phenological patterns of terrestrial plants. *Annual Review of*  
1052 *Ecology and Systematics*, 16, 179–214.

1053 Reich, P. B. (1995). Phenology of tropical forests: patterns, causes, and consequences. *Canadian*  
1054 *Journal of Botany*, 73, 164–174.

1055 Reich, P. B. (2014). The world-wide “fast–slow” plant economics spectrum: a traits manifesto.  
1056 *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

1057 Reich, P. B., & Borchert, R. (1984). Water stress and tree phenology in a tropical dry forest in  
1058 the lowlands of Costa Rica. *Journal of Ecology*, 72(1), 61–74.

1059 Restrepo-Coupe, N., da Rocha, H. R., Hutyra, L. R., da Araujo, A. C., Borma, L. S.,  
1060 Christoffersen, B., et al. (2013). What drives the seasonality of photosynthesis across the  
1061 Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux  
1062 network, 182-183, 128–144. <https://doi.org/10.1016/j.agrformet.2013.04.031>

1063 Restrepo-Coupe, N., Levine, N. M., Christoffersen, B. O., Albert, L. P., Wu, J., Costa, M. H., et  
1064 al. (2017). Do dynamic global vegetation models capture the seasonality of carbon fluxes in

1065 the Amazon basin? A data-model intercomparison. *Global Change Biology*, 23(1), 191–208.  
1066 <https://doi.org/10.1111/gcb.13442>

1067 Richardson, A. D., & O’Keefe, J. (2009). Phenological Differences Between Understory and  
1068 Overstory. In *Phenology of Ecosystem Processes* (pp. 87–117). New York, NY: Springer  
1069 New York. [https://doi.org/10.1007/978-1-4419-0026-5\\_4](https://doi.org/10.1007/978-1-4419-0026-5_4)

1070 Richardson, A. D., Anderson, R. S., Arain, M. A., Barr, A. G., Bohrer, G., Chen, G., et al.  
1071 (2012). Terrestrial biosphere models need better representation of vegetation phenology:  
1072 results from the North American Carbon Program Site Synthesis. *Global Change Biology*,  
1073 18(2), 566–584. <https://doi.org/10.1111/j.1365-2486.2011.02562.x>

1074 Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami,  
1075 P., et al. (2013a). Seasonal dynamics and age of stemwood nonstructural carbohydrates in  
1076 temperate forest trees. *New Phytologist*, 197(3), 850–861. <https://doi.org/10.1111/nph.12042>

1077 Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., et al.  
1078 (2018). Tracking vegetation phenology across diverse North American biomes using  
1079 PhenoCam imagery. *Scientific Data*, 5, 180028–24. <https://doi.org/10.1038/sdata.2018.28>

1080 Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M.  
1081 (2013b). Climate change, phenology, and phenological control of vegetation feedbacks to the  
1082 climate system. *Agricultural and Forest Meteorology*, 169, 156–173.  
1083 <https://doi.org/10.1016/j.agrformet.2012.09.012>

1084 Roff, D. A., & Fairbairn, D. J. (2007). The evolution of trade-offs: where are we? *Journal of*  
1085 *Evolutionary Biology*, 20(2), 433–447. <https://doi.org/10.1111/j.1420-9101.2006.01255.x>

1086 Rossi, S., Anfodillo, T., Čufar, K., Cuny, H. E., Deslauriers, A., Fonti, P., et al. (2013). A meta-  
1087 analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the

1088 northern hemisphere. *Annals of Botany*, 112(9), 1911–1920.

1089 <https://doi.org/10.1093/aob/mct243>

1090 Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: feast or famine?

1091 *Biological Journal of the Linnean Society*, 32(6), 764–775.

1092 <https://doi.org/10.1093/treephys/tpr143>

1093 Saleska, S. R., Wu, J., Guan, K., Araújo, A. C., Huete, A., Nobre, A. D., & Restrepo-Coupe, N.

1094 (2016). Dry-season greening of Amazon forests. *Nature*, 531(7594), E4–E5.

1095 <https://doi.org/10.1038/nature16457>

1096 Samanta, A., Knyazikhin, Y., Xu, L., Dickinson, R. E., Fu, R., Costa, M. H., et al. (2012).

1097 Seasonal changes in leaf area of Amazon forests from leaf flushing and abscission. *Journal*

1098 *of Geophysical Research*, 117, G01015. <https://doi.org/10.1029/2011JG001818>

1099 Schwartz, M. (2013). Phenology: An Integrative Environmental Science. Springer Science &

1100 Business Media.

1101 Schwartz, M. D., AHAS, R., & AASA, A. (2006). Onset of spring starting earlier across the

1102 Northern Hemisphere. *Global Change Biology*, 12(2), 343–351.

1103 <https://doi.org/10.1111/j.1365-2486.2005.01097.x>

1104 Schwartz, M. D., Betancourt, J. L., & Weltzin, J. F. (2012). From Caprio's lilacs to the USA

1105 National Phenology Network. *Frontiers in Ecology and the Environment*, 10(6), 324–327.

1106 <https://doi.org/10.1890/110281>

1107 Sheil, D. (1997). Long-term growth and rainfall in a Ugandan moist forest: seasonal rhythms and

1108 flexing stems. *The Commonwealth Forestry Review*, 76(2), 121–127.

1109 <https://doi.org/10.2307/42608796>

1110

1111 Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., & Teste, F. P. (2012).  
1112 Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews*, 26(1),  
1113 39–60. <https://doi.org/10.1016/j.fbr.2012.01.001>

1114 Smith, M. N., Stark, S. C., Taylor, T. C., Ferreira, M. L., de Oliveira, E., Restrepo-Coupe, N., et  
1115 al. (2019). Seasonal and drought related changes in leaf area profiles depend on height and  
1116 light environment in an Amazon forest. *New Phytologist*, nph.15726–nph.15734.  
1117 <https://doi.org/10.1111/nph.15726>

1118 Smith-Ramirez, C., Armesto, J., & Figueroa, J. (1998). Flowering, fruiting and seed germination  
1119 in Chilean rain forest myrtaceae: ecological and phylogenetic constraints. *Plant Ecology*,  
1120 136(2), 119–131.

1121 Spellman, K. V., & Mulder, C. P. H. (2016). Validating Herbarium-Based Phenology Models  
1122 Using Citizen-Science Data. *BioScience*, 66(10), 897–906.  
1123 <https://doi.org/10.1093/biosci/biw116>

1124 Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, 3(3), 259–268.

1125 Steinaker, D. F., & Wilson, S. D. (2008, November). Phenology of fine roots and leaves in forest  
1126 and grassland. *Journal of Ecology*, 96(6), 1222–1229. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2745.2008.01439.x)  
1127 [2745.2008.01439.x](https://doi.org/10.1111/j.1365-2745.2008.01439.x)

1128 Strahler, A. H., & Strahler, A. (2006). *Introducing Physical Geography* (4 ed.). John Wiley &  
1129 Sons Incorporated.

1130 Tang, H., & Dubayah, R. (2017). Light-driven growth in Amazon evergreen forests explained by  
1131 seasonal variations of vertical canopy structure. *Proceedings of the National Academy of*  
1132 *Sciences of the United States of America*, 114(10), 2640–2644.  
1133 <https://doi.org/10.1073/pnas.1616943114>

1134 Teskey, R. O., & Hinckley, T. M. (1981). Influence of temperature and water potential on root  
1135 growth of white oak. *Physiologia Plantarum*, 52, 363–369.

1136 Thomas, S. C., & Winner, W. E. (2002). Photosynthetic differences between saplings and adult  
1137 trees: an integration of field results by meta-analysis. *Tree Physiology*, 22, 117–127.

1138 Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological  
1139 relevance: a review, 372(1723), 20160135–20160113.  
1140 <https://doi.org/10.1098/rstb.2016.0135>

1141 Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., et al. (2007). Factors  
1142 controlling CO<sub>2</sub> exchange on timescales from hourly to decadal at Harvard Forest. *Journal of*  
1143 *Geophysical Research*, 112(G2), G02020. <https://doi.org/10.1029/2006JG000293>

1144 van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests:  
1145 adaptive significance and consequences for primary consumers. *Annual Review of Ecology*  
1146 *and Systematics*, 24, 353–377. <https://doi.org/10.1146/annurev.es.24.110193.002033>

1147 Virjamo, V., & Julkunen-Tiitto, R. (2014). Shoot development of Norway spruce (*Picea abies*)  
1148 involves changes in piperidine alkaloids and condensed tannins. *Trees*, 28(2), 427–437.  
1149 <https://doi.org/10.1007/s00468-013-0960-3>

1150 Wagner, F. H., Hérault, B., Bonal, D., Stahl, C., Anderson, L. O., Baker, T. R., et al. (2016).  
1151 Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests,  
1152 13(8), 2537–2562. <https://doi.org/10.5194/bg-13-2537-2016-supplement>

1153 Wagner, F., Rossi, V., Stahl, C., Bonal, D., & Hérault, B. (2013). Asynchronism in leaf and  
1154 wood production in tropical forests: a study combining satellite and ground-based  
1155 measurements. *Biogeosciences*, 10(11), 7307–7321. [https://doi.org/10.5194/bg-10-7307-](https://doi.org/10.5194/bg-10-7307-2013)  
1156 2013

1157 Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., et al.  
1158 (2016). Leaf development and demography explain photosynthetic seasonality in Amazon  
1159 evergreen forests. *Science*, *351*(6276), 972–976. <https://doi.org/10.1126/science.aad5068>  
1160 Wu, J., Chavana-Bryant, C., Prohaska, N., Serbin, S. P., Guan, K., Albert, L. P., et al. (2017).  
1161 Convergence in relationships between leaf traits, spectra and age across diverse canopy  
1162 environments and two contrasting tropical forests. *The New Phytologist*, *214*(3), 1033–1048.  
1163 <https://doi.org/10.1111/nph.14051>  
1164 Würth, M. K. R., Peláez-Riedl, S., Wright, S. J., & Korner, C. (2005). Non-structural  
1165 carbohydrate pools in a tropical forest. *Oecologia*, *143*(1), 11–24.  
1166 <https://doi.org/10.1007/s00442-004-1773-2>  
1167 Yang, L. H., & Rudolf, V. H. W. (2010). Phenology, ontogeny and the effects of climate change  
1168 on the timing of species interactions. *Ecology Letters*, *13*(1), 1–10.  
1169 <https://doi.org/10.1111/j.1461-0248.2009.01402.x>  
1170