



HAL
open science

Cryptic phenology in plants: Case studies, implications, and recommendations

Loren Albert, Natalia Restrepo-coupe, Marielle Smith, Jin Wu, Cecilia Chavana-bryant, Neill Prohaska, Tyeen Taylor, Giordane Martins, Philippe Ciais, Jiafu M Mao, et al.

► **To cite this version:**

Loren Albert, Natalia Restrepo-coupe, Marielle Smith, Jin Wu, Cecilia Chavana-bryant, et al.. Cryptic phenology in plants: Case studies, implications, and recommendations. *Global Change Biology*, 2019, 25 (11), pp.3591-3608. 10.1111/gcb.14759 . hal-02899482

HAL Id: hal-02899482

<https://hal.science/hal-02899482>

Submitted on 16 Jun 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1

2 DR. LOREN ALBERT (Orcid ID : 0000-0002-9674-6071)

3 DR. NATALIA RESTREPO-COUBE (Orcid ID : 0000-0003-3921-1772)

4 DR. MARIELLE N SMITH (Orcid ID : 0000-0003-2323-331X)

5 DR. WEI LI (Orcid ID : 0000-0003-2543-2558)

6

7

8 Article type : Research Review

9

10

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

12

13 **Running title:** Cryptic phenology in plants

14

15 **Authors:**16 Loren P. Albert^{1,2}, Natalia Restrepo-Coupe^{1,3}, Marielle N. Smith¹, Jin Wu^{4,5}, Cecilia Chavana-17 Bryant^{6,7,8}, Neill Prohaska¹, Tyeen C. Taylor¹, Giordane A. Martins⁹, Philippe Ciais¹⁰, Jiafu18 Mao¹², M. Altaf Arain¹³, Wei Li^{10,11}, Xiaoying Shi¹², Daniel M. Ricciuto¹², Travis E. Huxman¹⁴,19 Sean M. McMahon¹⁵, Scott R. Saleska¹

20

21 **Affiliations:**22 ¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721,

23 USA

24 ²Institute at Brown for Environment and Society, Brown University, Providence, RI 02912, USA25 ³School of Life Science, University of Technology Sydney, Ultimo, NSW, Australia26 ⁴Biological, Environmental & Climate Sciences Department, Brookhaven National Lab, Upton,

27 New York, NY 11973, USA

28 ⁵School of Biological Sciences, The University of Hong Kong, Pokfulam, Hong Kong29 ⁶Environmental Change Institute, School of Geography and the Environment, University of

30 Oxford, Oxford, UK

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/GCB.14759](https://doi.org/10.1111/GCB.14759)

This article is protected by copyright. All rights reserved

31 ⁷Climate & Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, 1
32 Cyclotron Road, Berkeley, CA, 94720, USA
33 ⁸Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA,
34 94720, USA
35 ⁹Ciências de Florestas Tropicais, Instituto Nacional de Pesquisas da Amazônia (INPA), CEP
36 69.067-375, Manaus, AM, Brazil.
37 ¹⁰Laboratoire des Sciences du Climat et de l'Environnement, 91191 Gif sur Yvette, France
38 ¹¹Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth
39 System Science, Tsinghua University, Beijing, China
40 ¹²Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National
41 Laboratory, Oak Ridge, TN, 37831-6301, USA
42 ¹³School of Geography and Earth Sciences & McMaster Centre for Climate Change, McMaster
43 University, Hamilton, Ontario, L8S 4K1 Canada
44 ¹⁴Ecology and Evolutionary Biology & Center for Environmental Biology, University of
45 California, Irvine, CA 92697, USA
46 ¹⁵Smithsonian Institution's Forest Global Earth Observatory & Smithsonian Environmental
47 Research Center, Edgewater, MD, 21037, USA

48
49 **Key words:** climate change, plant ecology, plant physiology, seasonality, terrestrial biosphere
50 models, dynamic global vegetation models, whole plant biology

51
52 **Corresponding authors:**
53 Loren Albert
54 Address: Brown University; Institute at Brown for Environment and Society; 85 Waterman
55 Street; Providence, RI, 02912
56 Email: lalbert@email.arizona.edu Phone: (832) 266-3051 Fax: N/A
57 Scott Saleska
58 Address: The University of Arizona; Department of Ecology & Evolutionary Biology; P.O. Box
59 210088; Tucson, AZ, 85721
60 Email: saleska@email.arizona.edu Phone: (520) 626-5838 Fax: N/A

61

This article is protected by copyright. All rights reserved

62 **Statement of authorship:**

63 LA organized and wrote the paper with advice/input from SMM, TEH and SRS. NRC
64 contributed earth system model runs for the tropical forest case study at K67 and compiled
65 comparison data into figures. MNS reviewed, synthesized and illustrated published LAI and
66 litterfall data. For the temperate forest case study at Harvard Forest, SMM contributed DBH and
67 allometry, and PC, AA, JM, WL, DMR, and XS contributed model runs and feedback on the
68 manuscript. NRC, MNS, JW, SM, SRS, NP, TCT and CCB contributed text and feedback for
69 their areas of expertise.

70

71 **Conflict of interest statement:** The authors declare no conflict of interest.

72 **ABSTRACT**

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

88 **INTRODUCTION**

89 All organisms have physical limits beyond which they function poorly or perish, and face trade-
90 offs in the allocation of finite resources to different structures and functions (Araújo et al., 2013;
91 Bennett & Lenski, 2007). Evolutionary strategies to establish, survive, grow, and reproduce are
92 shaped by such fundamental constraints and trade-offs (Roff & Fairbairn, 2007; Stearns, 1989).

93 When physical constraints or available resources vary regularly through time, organisms often
94 evolve temporal patterns in their activities to match or complement these variations (Diamond,
95 Frame, Martin, & Buckley, 2011). Temporal rhythms can also arise from time-dependent
96 biological process such as ontogeny and demography (Niinemets, García-Plazaola, & Tosens,
97 2012; Thomas & Winner, 2002). The Earth surface experiences seasonal cycles in temperature,
98 precipitation, and light that influence the availability of resources and the potential to carry out
99 the chemistry underlying biological processes (Schwartz, 2013; A. H. Strahler & Strahler, 2006).
100 Sessile organisms, such as most multicellular plants, are subjected to these seasonal cycles in-
101 place. Plant phenology—the timing of cyclic or recurrent biological events in plants—represents
102 functional strategies to persist within the bounds of natural climate seasonality and biological
103 possibility (Forrest & Miller-Rushing, 2010; Rathcke & Lacey, 1985). The study of phenology
104 has thus long been used as a means for gaining insight into the ecology and evolution of plants
105 and other organisms (Lieth, 1974).

106 The term ‘phenology’ traces to the Greek root *phaino*, meaning ‘to show,’ or ‘to appear’
107 (Schwartz, 2013), and early influential works on phenology promoted observations of
108 phenomena that were ‘sharp,’ ‘visible,’ and easy to detect (Leopold & Jones, 1947). In today’s
109 lexicon, common definitions of phenology broadly encompass the timing of cyclic or recurrent
110 biological events in plants, along with the causes and consequences of that timing (e.g. Lieth
111 1974, and (*phenology, n.* : *Oxford English Dictionary*, 2005). In contrast with broad
112 contemporary definitions of phenology, studies of phenology often reflect the origin and history
113 of the term by focusing on readily apparent biological events. These are generally aboveground
114 and accompanied by changes that are readily and reproducibly distinguished with human senses
115 such as visible changes in color, position, mass and volume. In plants, these include phenomena
116 such as germination in annual plants, synchronized leaf production (leaf flush) and abscission in
117 deciduous forests (Murali & Sukumar, 1993; Richardson & O’Keefe, 2009), and the onset of
118 anthesis (flower opening) (Schwartz, 2013). Some phenological patterns, such as deciduous
119 forest leaf onset, are also apparent at canopy and larger spatial scales with remote sensing tools
120 ranging from phenocams to satellites (Badeck et al., 2004; Buitenwerf, Rose, & Higgins, 2015).
121 Studying the timing and controls of such apparent biological events has contributed to
122 understanding the evolution of plant traits and strategies in response to cycles in temperature,
123 precipitation, photoperiod, and other physical variables (Chuine, 2010; Z. Huang, Liu, Bradford,

124 Huxman, & Venable, 2016; Pau et al., 2011; van Schaik, Terborgh, & Wright, 1993).
125 Phenological studies have also advanced our understanding of ecology, as many phenological
126 patterns are coupled to biotic interactions such as intra-annual dynamics of predator or mutualist
127 populations (Pau et al., 2011; Schwartz, 2013). More recently, some phenological events, such as
128 date of anthesis or first leaf emergence, have proven useful indicators of biological responses to
129 climate change (e.g. Parmesan & Yohe, 2003), and the relative ease of observing such events has
130 enabled citizen science at regional and continental scales (Schwartz, Betancourt, & Weltzin,
131 2012).

132 However, many processes in plants are *not* readily apparent, but are no less cyclic or
133 seasonal than the more easily observed phenomena that humans have historically monitored.
134 These phenologies are what might be called ‘cryptic.’ Some phenological patterns are difficult to
135 detect because they are hidden, including below-ground activities such as allocation to roots, and
136 internal processes such as allocation to carbohydrate reserves or cell differentiation. Other
137 phenological patterns are missed or misinterpreted based on common measurements at typical
138 scales of examination (e.g. changes in mass, area or volume of plant organs or of biomass pools).
139 Cryptic phenologies are not as well understood as apparent phenologies, and they have not been
140 used as indicators of climate change. Yet phenologies, including cryptic phenologies, play
141 critical roles in ecosystems, and mediate large-scale fluxes of carbon, nutrients, water, and
142 energy that are essential to consider as Earth’s climate changes (Abramoff & Finzi, 2015;
143 McCormack, Adams, Smithwick, & Eissenstat, 2014; Noormets, 2009; Richardson, Keenan, et
144 al., 2013b).

145 To address the disparity between the narrow scope of apparent phenology and the much
146 broader scope of cyclic and seasonal plant activities, we first offer a framework with terminology
147 that identifies the underlying challenges to observing, interpreting, and modeling cryptic
148 phenologies. Then, focusing on trees, we review specific case studies in which missing cryptic
149 phenology leads to problems for understanding and modeling seasonal ecosystem processes:
150 wood allocation in a temperate mixed forest, and leaf phenology in tropical evergreen Amazon
151 forests. We emphasize that attention to cryptic phenology is timely because many terrestrial
152 biosphere models (TBMs, the models used to represent vegetation of the land surface in Earth
153 system models and needed for climate change predictions; Fisher, Huntzinger, Schwalm, &
154 Sitch, 2014), assume that cryptic phenologies are strongly correlated with apparent phenologies,

155 and that such assumptions can lead to misattribution of the causes behind observed fluxes of
156 carbon, water, nutrients, and energy. Although we focus on trees, we argue that cryptic
157 phenologies are ubiquitous, and their conceptualization, characterization, and interpretation are
158 essential for accurate prediction at scales from organisms to ecosystems across the globe.

159

160 **THE CHALLENGE OF CRYPTIC PHENOLOGY: A FRAMEWORK**

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

169 Plant phenological patterns are *hidden* when some physical or technological barrier
170 obstructs observation (Table 1). Soil conceals below-ground processes such as cycles of root
171 production and turn-over (Abramoff & Finzi, 2015; Delpierre et al., 2016). Internal plant
172 structures are (by definition) hidden behind layers of cells, making the timing of recurrent
173 processes such as secondary xylem (wood) formation difficult to observe *in vivo* (Chaffey, 1999;
174 Plomion, Leprovost, & Stokes, 2001). Large-scale phenological processes can also be hidden, as
175 cloud cover can consistently obstruct satellite observations of vegetation reflectance over humid
176 regions such as tropical forests (Asner, 2001). In dense forests, the upper canopy leaves partly
177 obstruct remote sensing observations of mid- and understory leaf area patterns (Tang &
178 Dubayah, 2017) and vice versa for ground-based observations, (Smith et al., 2019). When
179 phenological processes are hidden, describing them often requires time-consuming methods,
180 such as minirhizotrons or soil cores (for roots; Abramoff & Finzi, 2015; Gaudinski et al., 2010),
181 fixation of tissue samples from multiple time periods (for wood formation; Arend & Fromm,
182 2007), or ‘ground truth’ observations (for remotely-sensed vegetation greenness indices;
183 Chavana-Bryant et al., 2017; Lopes et al., 2016; Richardson et al., 2018; Wu et al., 2017).
184 Hidden phenological patterns are challenging and/or time-consuming to measure, but the
185 scientific community frequently acknowledges the scarcity of these measurements, and models

186 including hidden phenology explicitly define their representation within allocation schemes (e.g.
187 Abramoff & Finzi, 2015).

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

207 Whereas hidden phenological patterns are often acknowledged to exist, but rarely
208 measured, ambiguous phenological patterns are not frequently acknowledged because
209 measurements *are* being made—the challenge lies in interpreting those measurements. For
210 example, we understand that root phenology is hidden, and difficult to measure, because roots
211 are underground. By contrast, we may not even realize that leaf production and loss show
212 seasonal rhythms if the quantity of leaves in a canopy is largely constant (a compensatory
213 scenario). The distinction between hidden and ambiguous categories is not absolute because
214 phenology could be both hidden and ambiguous. For example, the mechanism of biomass gain
215 (xylogenesis) is hidden within stems, and stem diameter represents an integration of cells at
216 different stages in the sequence of xylogenesis: cell expansion, secondary cell wall thickening,

217 lignification and dead cells (Cuny et al., 2015; Plomion et al., 2001). Thus changes in stem
218 diameter emerge from expansion as well as biomass gain (Cuny et al., 2015), resulting in some
219 ambiguity.

220 Cryptic phenologies do not follow fundamentally different rules than their more apparent
221 counterparts. Plant phenologies, in general, are consequences of biology, climatic seasonality,
222 and their interactions. Yet a focus on cryptic phenology challenges us to explicitly consider our
223 current observational blind spots. These blind spots may prevent us from gaining a
224 comprehensive understanding of organismal strategies and limitations in relation to their biology
225 and physical environment, with consequences for our understanding of population, community,
226 and ecosystem ecology. Ultimately, our ability to document, understand, and model the
227 component processes that contribute to large-scale biosphere/atmosphere exchange of CO₂ and
228 water vapor, impacts our ability to predict responses of natural systems to global change (Getz et
229 al., 2017; Noormets, 2009; Richardson et al., 2012).

230

231 **CASE STUDIES IN CRYPTIC PHENOLOGY**

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

247 processes can be necessary for correct attribution of cause and effect—and ultimately modeling
248 ecosystem processes—in many systems.

249

250 **Cryptic phenology of bole growth in temperate forests: implications for the timing of** 251 **carbon allocation to wood**

252 A TBM model-data comparison of bole growth at Harvard Forest, a temperate mixed forest site,
253 reveals the challenge of estimating and modeling the hidden phenology of biomass gain from
254 wood allocation. Wood is a major component of aboveground biomass (He et al., 2018), and is
255 important for characterizing fast versus slow growth strategies across species (Chave et al., 2009;
256 Reich, 2014). The intra-annual timing of wood allocation may show how carbon gain responds to
257 seasonal climate, and reveal periods of vulnerability or resilience to stress (Babst et al., 2014;
258 Battipaglia et al., 2010). The process of woody biomass gain (from xylogenesis) is hidden within
259 boles (Cuny et al. 2015), and tree or plot scale biomass cannot be directly measured without
260 harvesting trees (Clark & Kellner, 2012). Because of this, woody biomass gain is rarely
261 measured (Cuny et al. 2015). Aboveground biomass change, which includes non-wood
262 components such as leaves, can be estimated by measuring bole diameter growth increment for
263 use with taxa-specific allometric equations (Chave et al., 2014; Chojnacky, Heath, & Jenkins,
264 2014). This approach is used in both multi-year (e.g. McMahon, Parker, & Miller, 2010) and
265 seasonal studies (McMahon & Parker, 2015; Delpierre et al., 2016).

266 We asked whether TBMs captured the phenology of carbon allocation to wood, and the
267 phenology of carbon allocation to leaves, with equal success. We expected that TBMs would be
268 challenged to capture the phenology of carbon allocation to wood because it is hidden and hence
269 rarely measured at fine timescales, so there are few datasets available to improve, constrain, and
270 test models (Delpierre et al., 2016). By contrast, carbon allocation to leaves is more apparent,
271 particularly in forests with many deciduous tree species with spring leaf emergence and autumn
272 senescence. We used fine scale changes in bole diameter growth as an estimation of the net
273 primary productivity (NPP) allocated to wood (NPP_{wood}). The allometric regression equations
274 were applied to a bi-weekly time series of high accuracy diameter at breast height (DBH)
275 measurements from dendrometer bands (McMahon & Parker, 2015) for three tree species at
276 Harvard Forest (supporting information appendix S1). We estimated NPP allocated to leaves
277 (NPP_{leaf} , Fig. 2a) at Harvard Forest based on leaf area index and litterfall time series (J. W.

278 Munger, n.d.; W. Munger & Wofsy, 2018; Urbanski et al., 2007; supporting information
279 appendix S2). Resulting NPP_{leaf} and NPP_{wood} reveal that carbon investment in leaves and wood is
280 highest early in the growing season (Fig. 2). The peaks in simulated NPP_{leaf} were within days of
281 the estimated peak NPP_{leaf} (and close to leaf budburst, which typically occurs around May 6
282 (Keenan and Richardson, 2015). By contrast, simulated phenological patterns in wood-related
283 output variables from three TBMs showed greater variation (Fig. 2, appendix S3). While the
284 Community Land Model version 4.5 (CLM4.5) shows a peak close to that seen in the
285 observations (around the time of budburst, at May 5), the peak for ORCHIDEE_{TRUNK} and
286 CLASS are months later (August 1 and August 11 respectively).

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

300 Despite the limitations of the observations and models, the comparison suggests that
301 some models (like CLM 4.5) align moderately well with DBH-derived NPP_{wood} , while others lag
302 DBH-derived NPP_{wood} by months. This divergence in model behaviors highlights the importance
303 of understanding the mechanisms driving both simulated and observed phenologies. The timing
304 of allocation to biomass and wood-related variables in these TBMs is primarily determined by
305 the pattern of NPP across seasons. In ORCHIDEE for example, the allocation fractions to
306 different tissues primarily respond to environmental conditions: water, light, and nitrogen
307 (Krinner et al., 2005). For the wood allocation in ORCHIDEE, a fraction of NPP is
308 instantaneously allocated to sapwood, then sapwood biomass is converted into heartwood

309 biomass based on a one-year time constant (Krinner et al., 2005). Ultimately, model NPP is
310 controlled by site-specific climate conditions and representations of forest physiology (e.g. plant
311 functional type), including leaf phenological patterns (e.g. leaf onset/abscission).

312 In contrast with model representations, physiological and tree-ring studies suggest that
313 the mechanisms underlying wood phenology go beyond environmental controls to also include
314 ontogeny of wood cells (Cuny et al., 2015; Plomion et al., 2001) and priorities in allocation
315 through time (e.g. allocation of carbon to wood growth versus storage as nonstructural
316 carbohydrates; Richardson, Carbone, et al., 2013a). Xylem production and differentiation follow
317 a sequence, and shifts in one phase are associated with comparable shifts in successive phases
318 (Rossi et al., 2013). This sequence offers a mechanism for wood phenology to respond to
319 environmental conditions that are integrated over time—not just instantaneous drivers (Rossi et
320 al., 2013). This sequence may also play a role in determining when trees are vulnerable or
321 resilient to stress. For example, developing wood cells expand before their cell walls thicken
322 with carbon-rich polysaccharides and lignins, and late wood is more dense than early wood in
323 temperate species (Plomion et al., 2001), so trees at different stages in the sequence of wood
324 development could be more or less sensitive to drought stress. Testing and developing model
325 frameworks for such hypotheses is currently challenging because the timing of carbon allocation
326 to wood is hidden *in vivo*. More direct measurements of wood formation (e.g. Cuny *et al.* 2016),
327 and nonstructural carbohydrates (e.g. Newell, Mulkey, & Wright, 2002), synchronized with
328 frequent measurements of DBH and leaf phenological patterns, would help us to understand and
329 model controls over wood phenological patterns (Delpierre et al., 2016; Guillemot et al., 2017),
330 and how the timing of wood allocation relates to growth strategy, environmental fluctuations,
331 and other plant traits.

332

333 **Amazon evergreen forests: implications of cryptic phenology for seasonality of ecosystem** 334 **carbon fluxes**

335 The challenge of cryptic phenology is not confined to a particular plant organ. Amazon
336 evergreen forests near the equator offer a case study where leaf phenology is ambiguous. Much
337 of the Amazon basin experiences annual wet and dry seasons (Restrepo-Coupe et al., 2013), and
338 this regular seasonal variation in cloud cover and precipitation may select for phenological
339 strategies that match plant activities with resource availability (Doughty et al., 2014; Graham,

340 Mulkey, Kitajima, Phillips, & Wright, 2003; M. O. Jones, Kimball, & Nemani, 2014; van Schaik
341 et al., 1993). Most of the Amazon is remote, making ground-based observations of phenology
342 difficult, especially given the many observations needed to sample the high diversity of tree
343 species (Cardoso et al., 2017) and strategies (Reich, 1995). Observations of canopies from
344 satellites are often obstructed by clouds (Asner, 2001), difficult to interpret (Samanta et al.,
345 2012), and the subject of controversy surrounding technical artifacts and their correction (Huete
346 et al., 2006; Morton et al., 2014; Saleska et al., 2016). Yet many recent studies offer evidence
347 that leaf production, leaf abscission, wood production and root production exhibit annual
348 rhythms in Amazon forests (Doughty et al., 2014; Girardin, Malhi, & Doughty, 2016; Lopes et
349 al., 2016; Wagner et al., 2016).

350 Many TBMs seem to be missing these phenological processes (Restrepo-Coupe et al.,
351 2017). Evidence that TBMs are lacking adequate phenological representation comes from a
352 model inter-comparison for a network of ecosystem flux observations sites (eddy flux towers) in
353 Amazonia (Restrepo-Coupe, et al., 2017). For illustration, we discuss the contrasting cases of
354 equatorial versus southern evergreen forest sites in the Amazon basin of Brazil. At the equatorial
355 site (K67 in the Tapajós National Forest, Brazil), four TBMs showed significant divergence from
356 the estimated interannual pattern of whole-system photosynthetic fluxes (Fig. 3a, gross primary
357 productivity, (GPP; $\text{gC m}^{-2} \text{d}^{-1}$) and a metric of photosynthetic capacity, (Pc; $\text{gC m}^{-2} \text{d}^{-1}$) for K67;
358 (Restrepo-Coupe et al., 2017). The reason for the divergence is that modeled photosynthetic
359 patterns are driven by environmental variability -- measures of soil water stress in this case
360 (model calculated soil water stress index 'FSW' for K67, Fig. 3b-g) -- which suppresses GPP
361 during the long dry season. Yet the observed interannual pattern of photosynthesis in this
362 ecosystem appears to be driven by something beyond instantaneous responses to seasonal
363 climate fluctuations.

364 Since TBMs already include climatic seasonality, their failure to capture GPP seasonality
365 suggests that phenological processes operate at the equatorial site that are separate from the
366 instantaneous physiological responses already represented. Canopy phenological activity could
367 drive the observed GPP via two mechanisms: 1) dry season increases in quantity of canopy
368 leaves (quantified as leaf area index, or LAI) and/or 2) dry season increases in canopy
369 photosynthetic capacity on a per unit area basis (Lopes et al., 2016; Restrepo-Coupe et al., 2017;
370 Wu et al., 2016). Observations of leaf quantity (LAI) from equatorial Amazon sites show that

371 LAI varies little across seasons (e.g. Fig. 3c ‘LAI’ shows low seasonality at K67). Leaf turnover,
372 however, exhibits a dry season pulse (Fig. 3e,f: ‘NPP_{leaf}’ and ‘NPP_{litter-fall}’), suggesting that LAI
373 is maintained because leaf production compensates for near-simultaneous leaf fall during the dry
374 season. As a result, LAI exhibits modest seasonal variation relative to seasonal variation in leaf
375 litterfall and leaf flush (Fig. 4). The seasonality of total LAI also fails to represent within-canopy
376 dynamics, as compensatory leaf area patterns have been identified between the upper and lower
377 canopy levels at K67 (Smith et al., 2019). Since new (recently expanded) leaves have high rates
378 of photosynthesis, replacing old leaves with new leaves can increase photosynthetic capacity of
379 the canopy on a per unit area basis (Albert et al., 2018; Doughty & Goulden, 2008; Niinemets et
380 al., 2012; Pantin, Simonneau, & Muller, 2012; Wu et al., 2016). The combination of leaf
381 turnover and leaf age-dependent CO₂ assimilation capacity creates a scenario at K67 in which
382 ecosystem photosynthetic capacity varies more than LAI (Fig. 3b,c). Therefore, the observable
383 canopy total LAI time series does not fully capture phenological patterns of leaf turnover or the
384 resulting shifts in canopy photosynthetic capacity at this site (Fig. 5) because leaf phenology is
385 compensatory (Fig. 1c).

386 In contrast to the equatorial Amazon site, at a southern Amazon forest (Reserva Jarú,
387 RJA), observations and models coincide, with GPP and P_c declining during the dry season,
388 consistent with increasing water limitation as the dry season progresses (Fig. 3h,i,n). We lack an
389 observational time series of LAI and litterfall for the southern site, but remote sensing (GLAS
390 satellite lidar) suggests that in the southern Amazon, LAI decreases during the dry season (Tang
391 & Dubayah, 2017). Thus the equatorial (K67) and southern (RJA) Amazon sites appear to
392 include trees with different phenological strategies (Restrepo-Coupe et al., 2013). We
393 hypothesize that many trees in high water availability equatorial sites may be adapted to optimize
394 light use over time, synchronizing leaf production with the sunny dry season as a strategy for
395 increasing annual carbon gain (Restrepo-Coupe et al., 2017). The tree communities at southern
396 sites like RJA may experience a weaker peak in dry season sunlight (Restrepo-Coupe et al.,
397 2013), and may shed leaves during dry seasons to protect plant water status. This interpretation is
398 consistent with studies asserting that tropical evergreen forests produce new leaves during
399 periods of high light if they are not strongly water-limited (Doughty & Goulden, 2008; Graham
400 et al., 2003; Guan et al., 2015; M. O. Jones et al., 2014; Reich & Borchert, 1984; Restrepo-
401 Coupe et al., 2013; van Schaik et al., 1993; Wu et al., 2016). This continuum between

402 precipitation-driven and light-driven tropical evergreen forest phenological strategies is not
403 included in most TBMs, and therefore might account for some of the divergence in their GPP
404 projections (Restrepo-Coupe et al., 2017).

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

421

422 **IMPLICATIONS OF CRYPTIC PHENOLOGY FOR PREDICTION ACROSS SCALES**

423 Fine-scale processes, integrated over space and time, create large-scale exchanges of mass and
424 energy between the biosphere and the atmosphere (Monson & Baldocchi, 2014). Here we
425 consider some of the fine-scale processes associated with cryptic phenology that, scaled up, have
426 implications for our ability to understand, model, and predict biosphere-atmosphere interactions
427 under climate change.

428

429 *Organ scale*

430 Plant traits can show very high within-species variation due to phenology (Chavana-
431 Bryant et al., 2017), and this variation can surpass interspecific variation for some traits (Fajardo
432 & Siefert, 2016). Specifically, leaf development and aging is associated with changes in internal

433 leaf structure (Lim, Kim, & Gil Nam, 2007; Niinemets et al., 2012), concentrations of secondary
434 metabolites (Z. Liu et al., 1998; Virjamo & Julkunen-Tiitto, 2014), emissions of volatile organic
435 compounds (Alves, Harley, Goncalves, da Silva Moura, & Jardine, 2014; Niinemets et al., 2010),
436 and metabolic rates (Albert et al., 2018; Niinemets et al., 2012; Pantin et al., 2012). For the goal
437 of scaling fluxes from leaves to canopies, these many physiological changes associated with leaf
438 age suggest that distinguishing between constant leaf phenology and compensatory leaf
439 phenology is important not only for tropical forests (as we describe in the first case study above),
440 but for evergreen forests in general.

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

448

449 *Organismal scale*

450 Natural selection would be expected to favor coordination in the timing of resource acquisition
451 with resource storage and allocation (Sala, Woodruff, & Meinzer, 2012). Since selection acts at
452 the level of individuals, if we want to understand the adaptive value of phenological changes, we
453 need to understand how all plant organs function together, as a unit, through time. It is very
454 difficult to study ‘whole’ plants in the wild, especially woody plants. Few (if any) studies have
455 quantified the phenologies of all plant organs in wild woody plants to gain an integrated
456 organism-level perspective on phenology (but see Hu et al., (2010) for whole-tree carbon
457 assimilation during the growing season; see Würth, Peláez-Riedl, Wright, & Korner (2005) for
458 seasonal variation in non-structural carbohydrate pools by plant organ; and see Doughty et al.,
459 (2014) for an example plot-scale study of wood, fine root, and canopy phenology). Studies
460 examining phenologies of two organs suggest that phenology is often asynchronous across
461 organs (Abramoff & Finzi, 2015; Wagner, Rossi, Stahl, Bonal, & Hérault, 2013). Comparing
462 phenological patterns of roots and shoots frequently reveals offsets between maximum root
463 growth and shoot growth, and these offsets vary across biomes (Abramoff & Finzi, 2015). In

464 tropical forests, leaf and wood production is often asynchronous (Wagner et al., 2013). The onset
465 and/or termination of growth may also vary; roots in temperate deciduous white oak, for
466 example, continue to elongate in winter after senescence of leaves (Teskey & Hinckley, 1981).
467 Nonstructural carbohydrate reserves also show phenological patterns that are species-dependent
468 (Würth et al., 2005) and affected by phenological patterns of leaves (Palacio, Maestro, &
469 Montserratmarti, 2007). Rates of carbon use regulate carbon uptake in plants (sink-driven
470 photosynthesis; Fatichi, Leuzinger, & Korner, 2014), so phenological changes in carbon demand
471 should impact the timing of photosynthetic activity.

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

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

493

494 *Community scale*

495 As climate changes, many studies have demonstrated that phenological patterns shift,
496 impacting species interactions (CaraDonna, Iler, & Inouye, 2014; Memmott, Craze, Waser, &
497 Price, 2007; Miller-Rushing, Hoyer, Inouye, & Post, 2010; Polgar & Primack, 2011; Rafferty,
498 CaraDonna, & Bronstein, 2014; Yang & Rudolf, 2010). Fewer studies have probed how hidden
499 phenologies shape species interactions, or how those interactions may be changing. To do so
500 could reveal that phenology mediates impacts of species interactions on plant mortality,
501 reproduction, and metabolism. For example, the timing of insect outbreaks in relation to
502 nonstructural carbohydrate reserves (which are affected by the timing of leaf renewal) may
503 explain interspecific differences in tolerance to defoliation (Chen, Wang, Dai, Wan, & Liu,
504 2017). Further investigation into how species interactions affect hidden phenologies would help
505 gain a more complete understanding of the interplay between climate change, whole plant
506 physiology, and species interactions.

507

508 *Ecosystem to global scale*

509 Projections of Earth’s future climate are particularly sensitive to uncertainties in the land
510 carbon cycle (Friedlingstein et al., 2014). Improving representation of the land carbon cycle in
511 TBMs requires understanding the drivers of phenology, and the role of phenology in mediating
512 biosphere-atmosphere exchanges (Richardson, Keenan, et al., 2013b). Recognizing phenological
513 rhythms at scales from plant organs to communities is prerequisite to identifying their role in
514 large scale (ecosystem to global) cycling of carbon. For example, investigating the distribution of
515 root ages at different times of the year could elucidate larger scale autotrophic respiration or soil
516 resource acquisition processes (because root age affects root respiration and nutrient uptake
517 capacity; Bouma et al., 2001). TBMs which are calibrated to match current observations, but that
518 include inaccurate relationships between drivers and vegetation responses, risk making biased
519 predictions of forest response to future climate changes because they do not incorporate
520 underlying biological mechanisms (De Weirdt et al., 2012; Restrepo-Coupe et al., 2017).

521

522 **RECOMMENDATIONS FOR MEASURING AND MODELING CRYPTIC**

523 **PHENOLOGY**

524 **Recommendations for empirical research**

525 To reveal cryptic phenological patterns empirically, we need to consider the target, frequency,
526 and methods of measurements. We recommend complementing existing studies and
527 measurements of aboveground, clearly visible phenological changes with measurements of
528 hidden phenological changes (Table 1). Specifically, we need more time series of development
529 and growth of roots (e.g. Abramoff and Finzi 2015, McCormack et al 2014), and internal
530 structures (e.g. Cuny et al. 2015), to learn when leaf phenology directly fuels the phenological
531 patterns of other plant organs (and thus can represent them by proxy), and when it does not.
532 Building upon studies examining synchrony in phenology of multiple plant organs (Bazié et al.,
533 2017; Delpierre et al., 2016; Michelot, Simard, Rathgeber, Dufrene, & Damesin, 2012; Omondi,
534 Odee, Ongamo, Kanya, & Khasa, 2016; Perrin, Rossi, & Isabel, 2017; Wagner et al., 2013),
535 whole-plant phenology studies in which all plant organs and their associated processes
536 (acquisition and allocation of carbon, water, and nutrients) are continuously monitored in the
537 same individual plants across seasons could elucidate the relationship between the phenology of
538 plant organs with each other, and with climate, and test the representation of phenology for
539 various PFTs.

540 Revealing cryptic phenological patterns will require more studies explicitly testing
541 whether compensatory processes (Fig. 1c) mistaken for constancy (Fig. 1b) mislead our
542 interpretation of mass, area, or volume time series. To this end, sampling schemes need to go
543 beyond measuring mass, area or volume of plant organs or “pools” (in aggregate) to also
544 measure rates of inputs and outputs to and from organs/pools across time. (Since mass-balance
545 equations have three terms—inputs, outputs, and the accumulated pool—at least two must be
546 measured to obtain a single solution). For example, litterfall time series should be collected to
547 correspond with total leaf area time series. To examine the metabolic consequences of constant
548 versus compensating phenology, we need more (1) measurements of plant organ activity as
549 organs develop and age, and (2) experiments manipulating phenological status to test the
550 interaction between phenology and physiology (including photosynthesis and respiration) under
551 various treatments (e.g. drought, temperature, and herbivory). When a measured variable (e.g.
552 mass or volume) is the sum of multiple component variables (Fig. 1a) then those components
553 should be characterized (if possible) in tests for scenarios when the time series of the measured
554 variable is not aligned with that of the component variable of interest. Fourier analysis is a

555 promising tool for decomposing phenological cycles (Bush et al., 2016), and should be explored
556 for revealing phenology that is otherwise ambiguous.

557 Phenological events can happen quickly and vary across landscapes. Fine temporal and
558 spatial resolution will capture patterns that might otherwise be missed (e.g. Smith et al. 2019).
559 How we measure phenological patterns has moved beyond plant-level measurements to
560 landscape measurements as technology has evolved, and we need to continue expanding our
561 capacity for detecting plant phenological activity at multiple spatial scales (e.g. leaves to
562 canopies to landscapes). Remote sensing technologies offer valuable tools for gathering
563 phenological data on large spatial scales. Chlorophyll fluorescence remote sensing products
564 promise to test the physiological interpretation of ‘greenness’ from the more traditional MODIS
565 products (Guan et al., 2015; Lee et al., 2013; Porcar-Castell et al., 2014). Continuous or frequent
566 high resolution near-surface remote sensing instrumentation such as phenocams (Klosterman et
567 al., 2014; Lopes et al., 2016; Wu et al., 2016) and lidar (Calders et al., 2015) offer finer spatial
568 resolution data to complement and potentially validate satellite-based phenology-related
569 products.

570 Although satellite-derived products are valuable tool for phenology (e.g. Guan et al
571 2015), some phenological patterns remain cryptic when relying on remote sensing tools.
572 Reflectance-based indices from satellites reveal more about the phenological status of upper
573 canopy leaves and shoots than about the hidden phenological activity of roots, boles, and internal
574 plant processes. Further development of remote sensing tools may help reveal hidden
575 phenologies; for example, lidar can be used to estimate LAI at all canopy heights, helping infer
576 leaf phenological patterns for deeper canopy layers that are hidden from other sensors (Tang &
577 Dubayah, 2017). We urge more tests to evaluate when remote sensing signals do, and do not,
578 link to phenology, including time series of comparisons between remote sensing signals and
579 plant-level measurements (e.g. changes in leaf production or woody biomass). In addition, the
580 development of high-throughput methods for evaluating gene expression (Kris et al., 2007),
581 together with the growing databases of annotated genomes, offer the opportunity to complement
582 aboveground measurements with information about regulation of internal or below-ground
583 activities.

584

585 **Recommendations for model development**

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

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

608 Evaluations of uncertainty and sensitivity require first having model formulations of
609 phenology. As we have argued, study efforts are not uniform, and phenological patterns may be
610 cryptic such that they can only be resolved with multiple measurements (e.g. inputs and outputs
611 or multiple variables). In these cases, it may be difficult to find enough information to develop
612 phenology schemes. Model-data comparisons, with observational data coming from multiple
613 independent sources (and multiple organs) at multiple scales (e.g. eddy covariance time series,
614 and measurements of allocation in individuals) should help determine if an important
615 phenological process could be wholly missing from models. Joint model and empirical efforts

616 can then identify, characterize, model, and evaluate the importance of the excluded phenological
617 processes.

618 Finally, we emphasize the value of drawing upon empirical and theoretical ecology,
619 evolution, and physiology for the development and refinement of phenological models. In
620 systems where the temporal dynamics of plant acquisition and allocation have been shown to be
621 under selection to increase fitness within climatic and biological constraints, optimization models
622 may be useful (e.g. Caldararu, Purves, & Palmer, 2014; Kikuzawa, 1991; 1996), but they should
623 be expanded to include multiple resources (e.g. moisture and nutrient optimization in addition to
624 carbon), and trade-offs between multiple purposes, such as growth and reproduction (Iwasa,
625 2000). However, it is also important to recognize that life history imposes temporal structure
626 relevant to modelling at the seasonal time scale, such as timelines for recruitment, maturation,
627 and mortality in annual plants, or timelines for development of the photosynthetic apparatus in
628 new leaves with different lifespans. Thus, a valuable challenge will be to formalize demographic
629 and physiological timelines in models and test their impact on model sensitivity and uncertainty.

630

631 **CONCLUSION**

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

640

641 **ACKNOWLEDGEMENTS**

642 This work was supported in part by the U.S. Department of Energy (DOE) (#DE-SC0008383).
643 LPA thanks the Marshall Foundation of Arizona for dissertation support and the Institute at
644 Brown for Environment and Society for postdoctoral support. Amazon model-observation
645 comparisons were supported in part by the Gordon and Betty Moore Foundation and NASA
646 ROSES (Award Number: NNX17AF65G). SMM was supported by NSF grant EF1137366 and

647 NSF MSB ENSA 1638490. Computational support for CLASS-CTEM-N+ was provided by
648 SHARCNET at McMaster University, Hamilton, ON, Canada. J. Mao, X. Shi, and D. Ricciuto
649 are supported by the Terrestrial Ecosystem Science Scientific Focus Area (TES SFA) project
650 funded through the Terrestrial Ecosystem Science Program in the Climate and Environmental
651 Sciences Division (CESD) of the Biological and Environmental Research (BER) Program in the
652 US Department of Energy (DOE) Office of Science. The simulation of CLM4.5 used resources
653 of the Oak Ridge Leadership Computing Facility at the Oak Ridge National Laboratory, which is
654 supported by the Office of Science of the U.S. Department of Energy under Contract No. DE-
655 AC05-00OR22725. ORCHIDEE is a global land surface model developed at the IPSL institute in
656 France. The MSTMIP simulations were performed with the support of the GhG Europe FP7
657 grant with computing facilities provided by “LSCE” or “TGCC. JW was supported by the US
658 DOE contract No. DE-SC0012704 to Brookhaven National Laboratory. Authors are grateful to
659 David Orwig and Jay Aylward for the Harvard Forest stem map, and to Girardin et al. (2016) for
660 sharing LAI and litterfall data. Authors thank David D. Breshears, Russell K. Monson, and Greg
661 Barron-Gafford for comments on drafts.

662
663 **DATA AVAILABILITY STATEMENT:** The Harvard Forest data are available from DOI:
664 10.17190/AMF/1246059. The code for Fig. 2 is openly available in
665 <https://github.com/nataliacoupe/CrypticPhenologyPlants>.

666 667 REFERENCES

- 668 Abramoff, R. Z., & Finzi, A. C. (2015). Are above- and below-ground phenology in sync? *New*
669 *Phytologist*, 205, 1054–1061. <https://doi.org/10.1111/nph.13111>
- 670 Albert, L. P., Wu, J., Prohaska, N., de Camargo, P. B., Huxman, T. E., Tribuzy, E. S., et al.
671 (2018). Age-dependent leaf physiology and consequences for crown-scale carbon uptake
672 during the dry season in an Amazon evergreen forest. *New Phytologist*, 219(3), 870–884.
673 <https://doi.org/10.1111/nph.15056>
- 674 Alves, E. G., Harley, P., Goncalves, J. F. de C., da Silva Moura, C. E., & Jardine, K. (2014).
675 Effects of light and temperature on isoprene emission at different leaf developmental stages
676 of *Eschweilera coriacea* in central Amazon. *Acta Amazonica*, 44(1), 9–18.

- 677 Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L.
678 (2013). Heat freezes niche evolution. *Ecology Letters*, *16*(9), 1206–1219.
679 <https://doi.org/10.1111/ele.12155>
- 680 Arend, M., & Fromm, J. (2007). Seasonal change in the drought response of wood cell
681 development in poplar. *Tree Physiology*, *27*(7), 985–992.
- 682 Asner, G. P. (2001). Cloud cover in Landsat observations of the Brazilian Amazon. *International*
683 *Journal of Remote Sensing*, *22*(18), 3855–3862.
684 <https://doi.org/10.1080/01431160010006926>
- 685 Babst, F., Alexander, M. R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., et al. (2014). A tree-
686 ring perspective on the terrestrial carbon cycle. *Oecologia*, *176*(2), 307–322.
687 <https://doi.org/10.1007/s00442-014-3031-6>
- 688 Badeck, F.-W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., & Sitch, S.
689 (2004). Responses of spring phenology to climate change. *New Phytologist*, *162*(2), 295–
690 309. <https://doi.org/10.1111/j.1469-8137.2004.01059.x>
- 691 Battipaglia, G., De Micco, V., Brand, W. A., Linke, P., Aronne, G., Saurer, M., & Cherubini, P.
692 (2010). Variations of vessel diameter and $\delta^{13}\text{C}$ in false rings of *Arbutus unedo* L. reflect
693 different environmental conditions. *New Phytologist*, *188*(4), 1099–1112.
694 <https://doi.org/10.1111/j.1469-8137.2010.03443.x>
- 695 Bauer, M. C., Meyer, S. E., & Allen, P. S. (1998). A simulation model to predict seed dormancy
696 loss in the field for *Bromus tectorum* L. *Journal of Experimental Botany*, *49*(324), 1235–
697 1244. <https://doi.org/10.1093/jexbot/49.324.1235>
- 698 Bazié, P., Ky-Dembele, C., Jourdan, C., Rouspard, O., Zombré, G., & Bayala, J. (2017).
699 Synchrony in the phenologies of fine roots and leaves of *Vitellaria paradoxa* in different land
700 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)
701 [017-0135-0](https://doi.org/10.1007/s10457-017-0135-0)
- 702 Bellprat, O., & Doblus-Reyes, F. (2016). Attribution of extreme weather and climate events
703 overestimated by unreliable climate simulations. *Geophysical Research Letters*, *43*(5), 2158–
704 2164. <https://doi.org/10.1002/2015GL067189>
- 705 Bennett, A. F., & Lenski, R. E. (2007). An experimental test of evolutionary trade-offs during
706 temperature adaptation. *Proceedings of the National Academy of Sciences*, *104*(Supplement
707 1), 8649–8654. <https://doi.org/10.1073/pnas.0702117104>

708 Bouma, T. J., Yanai, R. D., Elkin, A. D., Hartmond, U., Flores-Alva, D. E., & Eissenstat, D. M.
709 (2001). Estimating age-dependent costs and benefits of roots with contrasting life span:
710 comparing apples and oranges. *New Phytologist*, *150*(3), 685–695.

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

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

717 Caldararu, S., Purves, D. W., & Palmer, P. I. (2014). Phenology as a strategy for carbon
718 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)
719 [763-2014](https://doi.org/10.5194/bg-11-763-2014)

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

724 CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a
725 subalpine plant community. *Proceedings of the National Academy of Sciences*, *111*(13),
726 4916–4921. <https://doi.org/10.1073/pnas.1323073111>

727 Cardoso, D., Särkinen, T., Alexander, S., Amorim, A. M., Bittrich, V., Celis, M., et al. (2017).
728 Amazon plant diversity revealed by a taxonomically verified species list. *Proceedings of the*
729 *National Academy of Sciences*, *114*(40), 10695–10700.
730 <https://doi.org/10.1073/pnas.1706756114>

731 Chaffey, N. (1999). Cambium: old challenges–new opportunities. *Trees-Structure and Function*,
732 *13*, 138–151.

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

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

- 739 Chave, J., Réjou-Méchain, M., Burquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., et
740 al. (2014). Improved allometric models to estimate the aboveground biomass of tropical
741 trees. *Global Change Biology*, 20(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>
- 742 Chen, Z., Wang, L., Dai, Y., Wan, X., & Liu, S. (2017). Phenology-dependent variation in the
743 non-structural carbohydrates of broadleaf evergreen species plays an important role in
744 determining tolerance to defoliation (or herbivory). *Nature Publishing Group*, 1–11.
745 <https://doi.org/10.1038/s41598-017-09757-2>
- 746 Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H. S., Suresh, H. S., & Sukumar, R. (2015).
747 Forest Ecology and Management. *Forest Ecology and Management*, 336(C), 129–136.
748 <https://doi.org/10.1016/j.foreco.2014.10.007>
- 749 Chojnacky, D. C., Heath, L. S., & Jenkins, J. C. (2014). Updated generalized biomass equations
750 for North American tree species. *Forestry*, 87(1), 129–151.
751 <https://doi.org/10.1093/forestry/cpt053>
- 752 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of*
753 *the Royal Society B: Biological Sciences*, 365(1555), 3149–3160.
754 <https://doi.org/10.1098/rstb.2010.0142>
- 755 Churkina, G., Schimel, D., Braswell, B. H., & Xiao, X. (2005). Spatial analysis of growing
756 season length control over net ecosystem exchange. *Global Change Biology*, 11, 1777–1787.
757 <https://doi.org/10.1111/j.1365-2486.2005.01012.x>
- 758 Clark, D. B., & Kellner, J. R. (2012). Tropical forest biomass estimation and the fallacy of
759 misplaced concreteness. *Journal of Vegetation Science*, 23(6), 1191–1196.
760 <https://doi.org/10.1111/j.1654-1103.2012.01471.x>
- 761 Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., et al. (2011). The
762 Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes
763 and vegetation dynamics. *Geoscientific Model Development*, 4(3), 701–722.
764 <https://doi.org/10.5194/gmd-4-701-2011>
- 765 Cleland, E., Chuine, I., Menzel, A., Mooney, H., & Schwartz, M. (2007). Shifting plant
766 phenology in response to global change. *Trends in Ecology & Evolution*, 22(7), 357–365.
767 <https://doi.org/10.1016/j.tree.2007.04.003>

768 Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A.
769 (2012). Timing of climate variability and grassland productivity. *Proceedings of the*
770 *National Academy of Sciences*, 109(9), 3401–3405. <https://doi.org/10.1073/pnas.1118438109>

771 Cuny, H. E., Rathgeber, C. B. K., Frank, D., Fonti, P., Mäkinen, H., Prislán, P., et al. (2015).
772 Woody biomass production lags stem-girth increase by over one month in coniferous forests.
773 *Nature Plants*, 15160. <https://doi.org/10.1038/nplants.2015.160>

774 De Weirdt, M., Verbeeck, H., Maignan, F., Peylin, P., Poulter, B., Bonal, D., et al. (2012).
775 Seasonal leaf dynamics for tropical evergreen forests in a process-based global ecosystem
776 model. *Geoscientific Model Development*, 5(5), 1091–1108. [https://doi.org/10.5194/gmd-5-](https://doi.org/10.5194/gmd-5-1091-2012)
777 [1091-2012](https://doi.org/10.5194/gmd-5-1091-2012)

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

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

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

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

790 Dietze, M. C., Sala, A., Carbone, M. S., Czimeczik, C. I., Mantooth, J. A., Richardson, A. D., &
791 Vargas, R. (2014). Nonstructural Carbon in Woody Plants. *Annual Review of Plant Biology*,
792 65(1), 667–687. <https://doi.org/10.1146/annurev-arplant-050213-040054>

793 Doughty, C. E., & Goulden, M. L. (2008). Seasonal patterns of tropical forest leaf area index and
794 CO₂ exchange. *Journal of Geophysical Research*, 113(October), G00B06.
795 <https://doi.org/10.1029/2007JG000590>

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

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

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

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

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

809 Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of
810 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B:*
811 *Biological Sciences*, 365(1555), 3101–3112. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2008.01367.x)
812 [2656.2008.01367.x](https://doi.org/10.1111/j.1365-2656.2008.01367.x)

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

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

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

823 Getz, W. M., Marshall, C. R., Carlson, C. J., Giuggioli, L., Ryan, S. J., Románach, S. S., et al.
824 (2017). Making ecological models adequate. *Ecology Letters*, 21(2), 153–166.
825 <https://doi.org/10.1111/ele.12893>

826 Girardin, C.A., Malhi, Y., Doughty, C. E., Metcalfe, D.B., Meir, P., del Aguila-Pasquel, J.,
827 Araujo-Murakami, A., da Costa, A.C., Silva-Espejo, J.E., Farfan Amezcuita, F. and
828 Rowland, L. (2016). Seasonal trends of Amazonian rainforest phenology, net primary

829 productivity, and carbon allocation. *Global Biogeochemical Cycles*, 30, 700–715.
830 [https://doi.org/10.1002/\(ISSN\)1944-9224](https://doi.org/10.1002/(ISSN)1944-9224)

831 Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover
832 limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons.
833 *Proceedings of the National Academy of Sciences*, 100(2), 572–576.
834 <https://doi.org/10.1073/pnas.0133045100>

835 Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., et al. (2015). Photosynthetic
836 seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*, 8(4),
837 284–289. <https://doi.org/10.1038/ngeo2382>

838 Guillemot, J., François, C., Hmimina, G., Dufrene, E., Martin-StPaul, N. K., Soudani, K., et al.
839 (2017). Environmental control of carbon allocation matters for modelling forest growth. *New*
840 *Phytologist*, 214(1), 180–193. <https://doi.org/10.1111/nph.14320>

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

844 Hardegree, S. P. (2006). Predicting Germination Response to Temperature. I. Cardinal-
845 temperature Models and Subpopulation-specific Regression. *Annals of Botany*, 97(6), 1115–
846 1125. <https://doi.org/10.1093/aob/mcl071>

847 He, H., Zhang, C., Zhao, X., Fousseni, F., Wang, J., Dai, H., et al. (2018). Allometric biomass
848 equations for 12 tree species in coniferous and broadleaved mixed forests, Northeastern
849 China. *Plos One*, 13(1), e0186226–16. <https://doi.org/10.1371/journal.pone.0186226>

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

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

857 Huang, Z., Liu, S., Bradford, K. J., Huxman, T. E., & Venable, D. L. (2016). The contribution of
858 germination functional traits to population dynamics of a desert plant community. *Ecology*,
859 97(1), 250–261.

860 Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyyra, L. R., et al.
861 (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research*
862 *Letters*, 33(6), L06405.

863 Huntzinger, D. N., Post, W. M., Wei, Y., Michalak, A. M., West, T. O., Jacobson, A. R., et al.
864 (2012). Ecological Modelling. *Ecological Modelling*, 232, 144–157.
865 <https://doi.org/10.1016/j.ecolmodel.2012.02.004>

866 Iwasa, Y. (2000). Dynamic optimization of plant growth. *Evolutionary Ecology Research*, 2,
867 437–455.

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

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

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

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

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

881 Klosterman, S. T., Hufkens, K., Gray, J. M., Melaas, E., Sonnentag, O., Lavine, I., et al. (2014).
882 Evaluating remote sensing of deciduous forest phenology at multiple spatial scales using
883 PhenoCam imagery. *Biogeosciences*, 11(16), 4305–4320. [https://doi.org/10.5194/bg-11-](https://doi.org/10.5194/bg-11-4305-2014)
884 [4305-2014](https://doi.org/10.5194/bg-11-4305-2014)

885 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., et al.
886 (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere
887 system. *Global Biogeochemical Cycles*, 19(1), GB1015.
888 <https://doi.org/10.1029/2003GB002199>

889 Kris, R. M., Felder, S., Deyholos, M., Lambert, G. M., Hinton, J., Botros, I., et al. (2007). High-
890 throughput, high-sensitivity analysis of gene expression in Arabidopsis. *Plant Physiology*,
891 *144*(3), 1256–1266. <https://doi.org/10.1104/pp.107.098681>

892 Le Quéré, C., Moriarty, R., Andrew, R. M., Peters, G. P., Ciais, P., Friedlingstein, P., et al.
893 (2015). Global carbon budget 2014. *Earth System Science Data*, *7*(1), 47–85.
894 <https://doi.org/10.5194/essd-7-47-2015>

895 Lee, J. E., Frankenberg, C., van der Tol, C., Berry, J. A., Guanter, L., Boyce, C. K., et al. (2013).
896 Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll
897 fluorescence. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1761),
898 20130171–20130171. <https://doi.org/10.1126/science.1184984>

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

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

903 Lim, P. O., Kim, H. J., & Gil Nam, H. (2007). Leaf Senescence. *Annual Review of Plant Biology*,
904 *58*(1), 115–136. <https://doi.org/10.1146/annurev.arplant.57.032905.105316>

905 Liu, Z., Carpenter, S. B., Bourgeois, W. J., Yu, Y., Constantin, R. J., Falcon, M., & Adams, J.
906 (1998). Variations in the secondary metabolite camptothecin in relation to tissue age and
907 season in *Camptotheca acuminata*. *Biological Journal of the Linnean Society*, *18*, 265–270.

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

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

914 McCormack, M. L., Adams, T. S., Smithwick, E. A. H., & Eissenstat, D. M. (2014). Variability
915 in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology*,
916 *95*(8), 2224–2235.

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

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

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

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

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

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

938 Migliavacca, M., Sonnentag, O., Keenan, T. F., Cescatti, A., O'Keefe, J., & Richardson, A. D.
939 (2012). On the uncertainty of phenological responses to climate change, and implications for
940 a terrestrial biosphere model. *Biogeosciences*, *9*(6), 2063–2083. [https://doi.org/10.5194/bg-](https://doi.org/10.5194/bg-9-2063-2012)
941 [9-2063-2012](https://doi.org/10.5194/bg-9-2063-2012)

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

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

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

950 Mullen, R. B., & Schmidt, S. K. (1993). Mycorrhizal infection, phosphorus uptake, and
951 phenology in *Ranunculus adoneus*: implications for the functioning of mycorrhizae in alpine
952 systems. *Oecologia*, 94(2), 229–234. <https://doi.org/10.1007/BF00341321>

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

955 Munger, W., & Wofsy, S. C. (2018). Biomass Inventories at Harvard Forest EMS Tower since
956 1993. <https://doi.org/10.6073/pasta/37ff12d47894a73ddd9d86c1225e2dc8>

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

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

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

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

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

968 Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., et al.
969 (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*,
970 18(3), 221–235. <https://doi.org/10.1111/ele.12399>

971 Omondi, S. F., Odee, D. W., Ongamo, G. O., Kanya, J. I., & Khasa, D. P. (2016). Synchrony in
972 Leafing, Flowering, and Fruiting Phenology of *Senegalia senegal* within Lake Baringo
973 Woodland, Kenya: Implication for Conservation and Tree Improvement. *International
974 Journal of Forestry Research*, 2016(4), 1–11. <https://doi.org/10.1155/2016/6904834>

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

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

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

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

987 Perrin, M., Rossi, S., & Isabel, N. (2017). Synchronisms between bud and cambium phenology
988 in black spruce: early-flushing provenances exhibit early xylem formation. *Tree Physiology*,
989 *37*(5), 593–603. <https://doi.org/10.1093/treephys/tpx019>

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

992 Plomion, C., Leprovost, G., & Stokes, A. (2001). Wood Formation in Trees. *Plant Physiology*,
993 *127*(4), 1513–1523. <https://doi.org/10.1104/pp.010816>

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

996 Porcar-Castell, A., Tyystjarvi, E., Atherton, J., van der Tol, C., Flexas, J., Pfundel, E. E., et al.
997 (2014). Linking chlorophyll a fluorescence to photosynthesis for remote sensing
998 applications: mechanisms and challenges. *Journal of Experimental Botany*, *65*(15), 4065–
999 4095. <https://doi.org/10.1093/jxb/eru191>

1000 Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a
1001 changing climate. *Journal of Experimental Botany*, *67*(12), 3617–3628.
1002 <https://doi.org/10.1093/jxb/erw062>

1003 Rafferty, N. E., CaraDonna, P. J., & Bronstein, J. L. (2014). Phenological shifts and the fate of
1004 mutualisms. *Oikos*, *124*(1), 14–21. <https://doi.org/10.1111/oik.01523>

1005 Rathcke, B., & Lacey, E. P. (1985). Phenological patterns of terrestrial plants. *Annual Review of*
1006 *Ecology and Systematics*, *16*, 179–214.

1007 Reich, P. B. (1995). Phenology of tropical forests: patterns, causes, and consequences. *Canadian*
1008 *Journal of Botany*, *73*, 164–174.

1009 Reich, P. B. (2014). The world-wide “fast–slow” plant economics spectrum: a traits manifesto.
1010 *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

1011 Reich, P. B., & Borchert, R. (1984). Water stress and tree phenology in a tropical dry forest in
1012 the lowlands of Costa Rica. *Journal of Ecology*, 72(1), 61–74.

1013 Restrepo-Coupe, N., da Rocha, H. R., Hutyrá, L. R., da Araujo, A. C., Borma, L. S.,
1014 Christoffersen, B., et al. (2013). What drives the seasonality of photosynthesis across the
1015 Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux
1016 network. *Agricultural and Forest Meteorology* 182-183, 128–144.
1017 <https://doi.org/10.1016/j.agrformet.2013.04.031>

1018 Restrepo-Coupe, N., Levine, N. M., Christoffersen, B. O., Albert, L. P., Wu, J., Costa, M. H., et
1019 al. (2017). Do dynamic global vegetation models capture the seasonality of carbon fluxes in
1020 the Amazon basin? A data-model intercomparison. *Global Change Biology*, 23(1), 191–208.
1021 <https://doi.org/10.1111/gcb.13442>

1022 Richardson, A. D., & O’Keefe, J. (2009). Phenological Differences Between Understory and
1023 Overstory. In *Phenology of Ecosystem Processes* (pp. 87–117). New York, NY: Springer
1024 New York. https://doi.org/10.1007/978-1-4419-0026-5_4

1025 Richardson, A. D., Anderson, R. S., Arain, M. A., Barr, A. G., Bohrer, G., Chen, G., et al.
1026 (2012). Terrestrial biosphere models need better representation of vegetation phenology:
1027 results from the North American Carbon Program Site Synthesis. *Global Change Biology*,
1028 18(2), 566–584. <https://doi.org/10.1111/j.1365-2486.2011.02562.x>

1029 Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami,
1030 P., et al. (2013a). Seasonal dynamics and age of stemwood nonstructural carbohydrates in
1031 temperate forest trees. *New Phytologist*, 197(3), 850–861. <https://doi.org/10.1111/nph.12042>

1032 Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., et al.
1033 (2018). Tracking vegetation phenology across diverse North American biomes using
1034 PhenoCam imagery. *Scientific Data*, 5, 180028–24. <https://doi.org/10.1038/sdata.2018.28>

1035 Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M.
1036 (2013b). Climate change, phenology, and phenological control of vegetation feedbacks to the
1037 climate system. *Agricultural and Forest Meteorology*, 169, 156–173.
1038 <https://doi.org/10.1016/j.agrformet.2012.09.012>

- 1039 Roff, D. A., & Fairbairn, D. J. (2007). The evolution of trade-offs: where are we? *Journal of*
1040 *Evolutionary Biology*, 20(2), 433–447. <https://doi.org/10.1111/j.1420-9101.2006.01255.x>
- 1041 Rossi, S., Anfodillo, T., Čufar, K., Cuny, H. E., Deslauriers, A., Fonti, P., et al. (2013). A meta-
1042 analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the
1043 northern hemisphere. *Annals of Botany*, 112(9), 1911–1920.
1044 <https://doi.org/10.1093/aob/mct243>
- 1045 Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: feast or famine?
1046 *Biological Journal of the Linnean Society*, 32(6), 764–775.
1047 <https://doi.org/10.1093/treephys/tpr143>
- 1048 Saleska, S. R., Wu, J., Guan, K., Araújo, A. C., Huete, A., Nobre, A. D., & Restrepo-Coupe, N.
1049 (2016). Dry-season greening of Amazon forests. *Nature*, 531(7594), E4–E5.
1050 <https://doi.org/10.1038/nature16457>
- 1051 Samanta, A., Knyazikhin, Y., Xu, L., Dickinson, R. E., Fu, R., Costa, M. H., et al. (2012).
1052 Seasonal changes in leaf area of Amazon forests from leaf flushing and abscission. *Journal*
1053 *of Geophysical Research*, 117, G01015. <https://doi.org/10.1029/2011JG001818>
- 1054 Schwartz, M. (2013). Phenology: An Integrative Environmental Science. Springer Science &
1055 Business Media.
- 1056 Schwartz, M. D., AHAS, R., & AASA, A. (2006). Onset of spring starting earlier across the
1057 Northern Hemisphere. *Global Change Biology*, 12(2), 343–351.
1058 <https://doi.org/10.1111/j.1365-2486.2005.01097.x>
- 1059 Schwartz, M. D., Betancourt, J. L., & Weltzin, J. F. (2012). From Caprio's lilacs to the USA
1060 National Phenology Network. *Frontiers in Ecology and the Environment*, 10(6), 324–327.
1061 <https://doi.org/10.1890/110281>
- 1062 Sheil, D. (1997). Long-term growth and rainfall in a Ugandan moist forest: seasonal rhythms and
1063 flexing stems. *The Commonwealth Forestry Review*, 76(2), 121–127.
1064 <https://doi.org/10.2307/42608796>
- 1065
- 1066 Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., & Teste, F. P. (2012).
1067 Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews*, 26(1),
1068 39–60. <https://doi.org/10.1016/j.fbr.2012.01.001>

- 1069 Smith, M. N., Stark, S. C., Taylor, T. C., Ferreira, M. L., de Oliveira, E., Restrepo-Coupe, N., et
1070 al. (2019). Seasonal and drought related changes in leaf area profiles depend on height and
1071 light environment in an Amazon forest. *New Phytologist*, *nph.15726–nph.15734*.
1072 <https://doi.org/10.1111/nph.15726>
- 1073 Smith-Ramirez, C., Armesto, J., & Figueroa, J. (1998). Flowering, fruiting and seed germination
1074 in Chilean rain forest myrtaceae: ecological and phylogenetic constraints. *Plant Ecology*,
1075 *136*(2), 119–131.
- 1076 Spellman, K. V., & Mulder, C. P. H. (2016). Validating Herbarium-Based Phenology Models
1077 Using Citizen-Science Data. *BioScience*, *66*(10), 897–906.
1078 <https://doi.org/10.1093/biosci/biw116>
- 1079 Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, *3*(3), 259–268.
- 1080 Steinaker, D. F., & Wilson, S. D. (2008). Phenology of fine roots and leaves in forest and
1081 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)
1082 [2745.2008.01439.x](https://doi.org/10.1111/j.1365-2745.2008.01439.x)
- 1083 Strahler, A. H., & Strahler, A. (2006). *Introducing Physical Geography* (4 ed.). John Wiley &
1084 Sons Incorporated.
- 1085 Tang, H., & Dubayah, R. (2017). Light-driven growth in Amazon evergreen forests explained by
1086 seasonal variations of vertical canopy structure. *Proceedings of the National Academy of*
1087 *Sciences of the United States of America*, *114*(10), 2640–2644.
1088 <https://doi.org/10.1073/pnas.1616943114>
- 1089 Teskey, R. O., & Hinckley, T. M. (1981). Influence of temperature and water potential on root
1090 growth of white oak. *Physiologia Plantarum*, *52*, 363–369.
- 1091 Thomas, S. C., & Winner, W. E. (2002). Photosynthetic differences between saplings and adult
1092 trees: an integration of field results by meta-analysis. *Tree Physiology*, *22*, 117–127.
- 1093 Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological
1094 relevance: a review, *Philosophical Transactions of the Royal Society B*, *372*(1723),
1095 *20160135–20160113*. <https://doi.org/10.1098/rstb.2016.0135>
- 1096 Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., et al. (2007). Factors
1097 controlling CO₂ exchange on timescales from hourly to decadal at Harvard Forest. *Journal of*
1098 *Geophysical Research*, *112*(G2), G02020. <https://doi.org/10.1029/2006JG000293>

- 1099 van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests:
1100 adaptive significance and consequences for primary consumers. *Annual Review of Ecology
1101 and Systematics*, 24, 353–377. <https://doi.org/10.1146/annurev.es.24.110193.002033>
- 1102 Virjamo, V., & Julkunen-Tiitto, R. (2014). Shoot development of Norway spruce (*Picea abies*)
1103 involves changes in piperidine alkaloids and condensed tannins. *Trees*, 28(2), 427–437.
1104 <https://doi.org/10.1007/s00468-013-0960-3>
- 1105 Wagner, F. H., Hérault, B., Bonal, D., Stahl, C., Anderson, L. O., Baker, T. R., et al. (2016).
1106 Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests,
1107 *Biogeosciences*, 13(8), 2537–2562. <https://doi.org/10.5194/bg-13-2537-2016>
- 1108 Wagner, F., Rossi, V., Stahl, C., Bonal, D., & Hérault, B. (2013). Asynchronism in leaf and
1109 wood production in tropical forests: a study combining satellite and ground-based
1110 measurements. *Biogeosciences*, 10(11), 7307–7321. [https://doi.org/10.5194/bg-10-7307-
1111 2013](https://doi.org/10.5194/bg-10-7307-2013)
- 1112 Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., et al.
1113 (2016). Leaf development and demography explain photosynthetic seasonality in Amazon
1114 evergreen forests. *Science*, 351(6276), 972–976. <https://doi.org/10.1126/science.aad5068>
- 1115 Wu, J., Chavana-Bryant, C., Prohaska, N., Serbin, S. P., Guan, K., Albert, L. P., et al. (2017).
1116 Convergence in relationships between leaf traits, spectra and age across diverse canopy
1117 environments and two contrasting tropical forests. *New Phytologist*, 214(3), 1033–1048.
1118 <https://doi.org/10.1111/nph.14051>
- 1119 Würth, M. K. R., Peláez-Riedl, S., Wright, S. J., & Korner, C. (2005). Non-structural
1120 carbohydrate pools in a tropical forest. *Oecologia*, 143(1), 11–24.
1121 <https://doi.org/10.1007/s00442-004-1773-2>
- 1122 Yang, L. H., & Rudolf, V. H. W. (2010). Phenology, ontogeny and the effects of climate change
1123 on the timing of species interactions. *Ecology Letters*, 13(1), 1–10.
1124 <https://doi.org/10.1111/j.1461-0248.2009.01402.x>

1125
1126
1127 Figure 1: Examples of ambiguous phenological patterns. In example 1 (a), multiple variables (Y
1128 and Z) contribute to some total that is measured. Variables Y and Z may have different peak
1129 timing, different rates of change, and/or different amplitudes, that become summed for the

1130 measured total. Thus the phenological patterns of individual variables Y and Z are ambiguous. In
1131 example 2 (b) and example 3 (c), the total for some biological variable X is the sum of an
1132 incoming (new) pool and outgoing (old) pool. In example 2, the total, the incoming, and the
1133 outgoing pools are constant. In example 3, the total is also constant, but the incoming and
1134 outgoing pools are dynamic, with inputs compensating for losses. Distinguishing between the
1135 scenarios represented by examples 2 and 3 is difficult based solely on measurements of the
1136 variable X total, and so phenological patterns of the incoming and outgoing pools remain
1137 ambiguous.

1138
1139 Figure 2: Seasonality of observed (black \pm gray standard deviation) versus model-simulated
1140 (colors) Net Primary Productivity (NPP) allocated to a) leaf biomass (NPP_{leaf}), and b) woody
1141 biomass (NPP_{wood}) metrics at a mixed deciduous evergreen temperate forest. NPP_{leaf} observations
1142 were calculated as $(dLAI/dt) \cdot LMA + \text{litterfall}$ where LAI is leaf area index and LMA is leaf mass
1143 per area. For models, NPP_{leaf} was calculated as the change in leaf biomass per unit time during
1144 the active part of the growing season: $(X_i - X_{i-1}) / (t_i - t_{i-1})$ where X is leaf biomass (in gC m^{-2}), t is
1145 time in days, and i is an index to each day. NPP_{wood} observations were from allometry using
1146 diameter-at-breast-height (DBH) increment measurements compared with outputs from three
1147 land surface models. For models, NPP_{wood} was calculated as biomass change per unit time in
1148 above ground woody biomass, as with NPP_{leaf} above, where X is the model output variable most
1149 comparable to aboveground woody biomass (in gC m^{-2}), t is time in days, , and i is an index to
1150 each day, for each model (which was vegetation biomass for CLASS, aboveground heartwood
1151 plus sapwood for ORCIDEE_{TRUNK}, and wood biomass for CLM4.5). Plot temporal resolution is
1152 16-day averages. The gray shaded area in all panels indicates the growing season, and the
1153 horizontal dotted line indicates zero. NPP_{leaf} simulations were not available for CLASS. Full
1154 NPP_{wood} estimation and model details are available in online supporting information.

1155
1156 Figure 3: Annual cycles of observed (black \pm gray standard deviation) versus model-simulated
1157 (colors) forest metrics in two Amazon forests (an equatorial Amazon forest, K67, and a southern
1158 Amazon forest, RJA), including (panels from top to bottom): daily average ecosystem-scale
1159 photosynthesis (GPP); daily average ecosystem-scale photosynthetic capacity (Pc, GPP at a fixed
1160 PAR range ($725\text{-}875\text{umol m}^{-2} \text{s}^{-1}$), vapor pressure deficit, air temperature and light quality

1161 measured as cloudiness index (all time mean \pm 1 standard deviation)); leaf area index (LAI); net
1162 primary productivity (NPP) allocated to leaves (leaf production; NPP_{leaf}); NPP going to litterfall
1163 ($\text{NPP}_{\text{litterfall}}$), and NPP allocated to wood (NPP_{wood}); soil water stress metric (FSW), where 1=no
1164 stress (Ju et al., 2006). Temporal resolution is 16-day averages. The light gray shaded box all
1165 panels represents the dry season. For K67 LAI data, we use data from the control plot of a close-
1166 by drought experiment (Juárez et al. 2007; Brando et al. 2010). LAI and NPP observations were
1167 not available for the RJA site. Lines are dashed for IBIS NPP to indicate that NPP is allocated
1168 only at the end of the year. For further details on model intercomparison, see Restrepo-Coupe et
1169 al. (2017).

1170 Figure 4: Leaf turnover is concealed by near-constant leaf area index (LAI), as shown by the
1171 seasonal canopy dynamics of LAI, leaf litterfall, and leaf production averaged across five
1172 Amazonian sites. The pulses of litterfall and leaf production support compensatory leaf
1173 phenology (Fig 1c) rather than constant leaf phenology (Fig 1b). Bars show mean values of
1174 annual amplitude scaled for studies ($n=5$ sites) of lowland evergreen tropical forests where both
1175 LAI and litterfall have been measured. Seasonal range is the annual amplitude scaled by mean
1176 value and is calculated as the difference between the maximum dry season value and the
1177 minimum wet season value, divided by the mean annual value (%). Error bars show standard
1178 deviation of the mean. Studies included in this figure: Tambopata-Candamo Reserve, south-
1179 eastern Peru (Girardin et al. 2016); Caxiuana, Floresta Nacional de Caxiuana, Pará, Brazil
1180 (Girardin et al. 2016); K83 (Doughty & Goulden 2008) and K67 (Brando et al. 2010 and
1181 Malhado et al. 2009) are located in the Tapajós National Forest, Pará, Brazil. Sites experience a
1182 range of mean annual precipitation values (1900 – 2572 mm).

1183 Figure 5: Illustration of how cryptic leaf turnover creates a phenological pattern in canopy
1184 photosynthetic capacity. (a) Individual crowns drop old leaves and produce new leaves with
1185 some degree of synchronization. Inset: leaf photosynthetic capacity depends upon leaf age. (b)
1186 The proportion of leaf area index belonging to previous year's growth (old leaves) and new leaf
1187 growth (new leaves) changes through the dry season. Here leaf phenology is difficult to detect
1188 because of compensatory inputs and outputs (see Fig. 1c). (c) the combination of leaf turnover
1189 and leaf ontogeny increase the canopy photosynthetic capacity, but neither total LAI nor
1190 satellite-based proxies for LAI and greenness show this same increase.

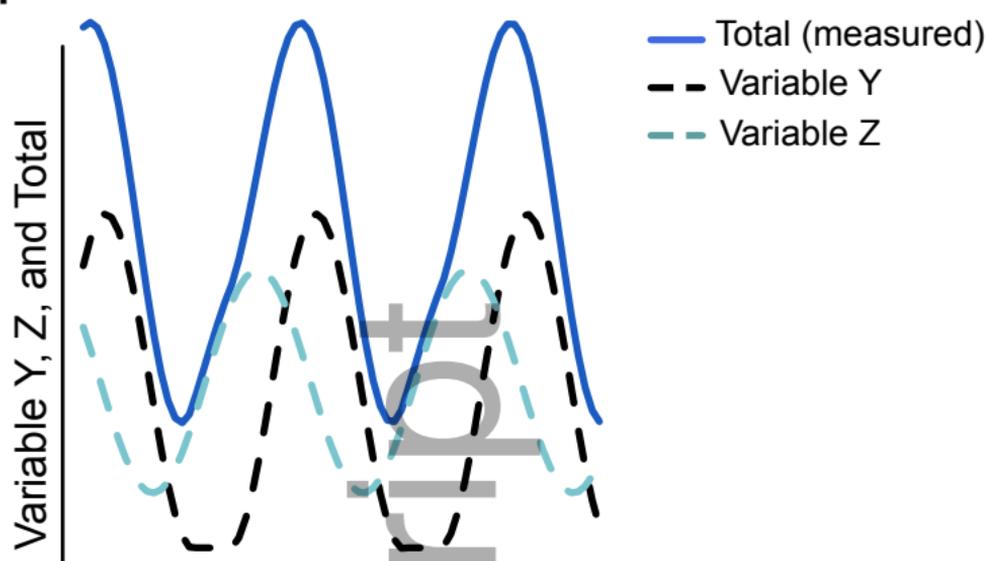
Author Manuscript

1192 Table 1. Categorization of plant phenologies based on our current capacity for successful measurement, observation, and/or interpretation.

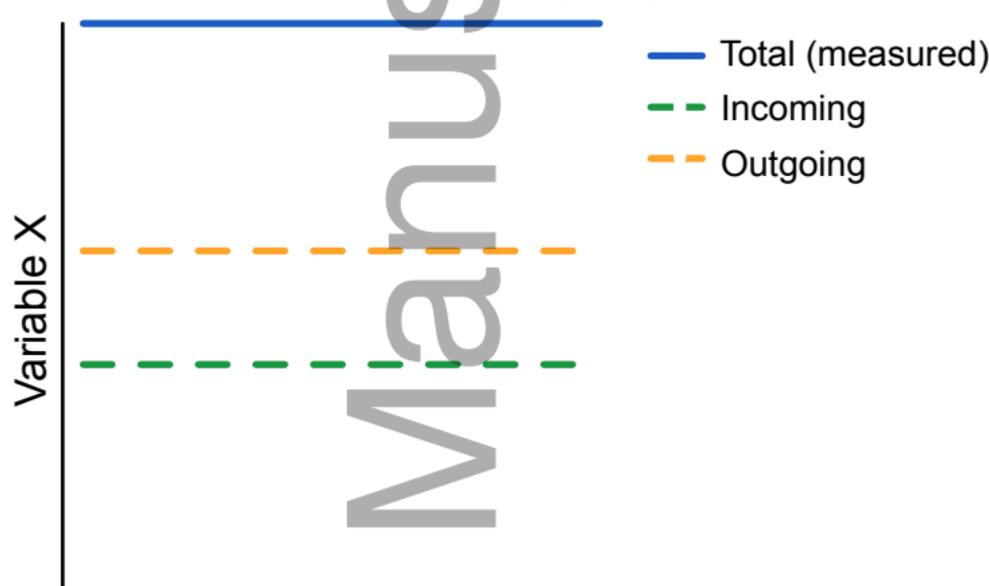
Plant phenology category	Specific examples	Frequently measured?	Model representation examples	Examples of current or possible use
<i>Apparent</i>				
Phases and events easily observed by humans.	<ul style="list-style-type: none"> • Bud burst¹ • Leaf abscission² • Anthesis³ • Fruit maturation⁴ 	Yes, and 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). ⁵	<ul style="list-style-type: none"> • Defining the duration of the growing season in seasonally dormant systems.^{6,7} • Testing capacity of hydrothermal models to predict events such as germination.^{8,9} • Using changes in timing of phenological events as indicators of climate change.^{10,11,12}
<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"> • Below-ground processes such as root production.^{13,14} • Structural changes within cells or tissues such as xylem formation.¹⁵ • Remote sensing in cloudy regions such as wet tropical forests.¹⁶ 	No, but these blind spots are generally acknowledged.	Often assumed to be linked to or dependent on apparent phenology. ^{17,18} This assumption is generally explicit.	<ul style="list-style-type: none"> • Modeling of whole plant carbon and water dynamics.^{19,20} • Estimating intra-annual cycles of biomass gain.¹⁵ • Identifying temporal variation in below-ground interactions and associations.^{21,22}
<i>Cryptic: ambiguous</i>				

-
- ¹ 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>
- ² (Escudero & Del Arco, 1987)
- ³ (Smith-Ramirez, Armesto, & Figueroa, 1998)
- ⁴ (Spellman & Mulder, 2016)
- ⁵ (Huntzinger et al., 2012)
- ⁶ (Churkina, Schimel, Braswell, & Xiao, 2005)}
- ⁷ (Schwartz, 2013)
- ⁸ (Bauer, Meyer, & Allen, 1998)
- ⁹ (Hardegree, 2006)
- ¹⁰ (Badeck et al., 2004)
- ¹¹ (Schwartz, AHAS, & AASA, 2006)
- ¹² (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007)
- ¹³ (Steinaker & Wilson, 2008)
- ¹⁴ (Radville, McCormack, Post, & Eissenstat, 2016)
- ¹⁵ (Cuny et al., 2015)
- ¹⁶ (Asner, 2001)
- ¹⁷ (Delpierre, Berveiller, Granda, & Dufrene, 2015)
- ¹⁸ (Abramoff & Finzi)
- ¹⁹ (Hu, Moore, Riveros-Iregui, Burns, & Monson, 2010)
- ²⁰ (Michelot et al., 2012)
- ²¹ (Mullen & Schmidt, 1993)
- ²² (S. W. Simard et al., 2012)

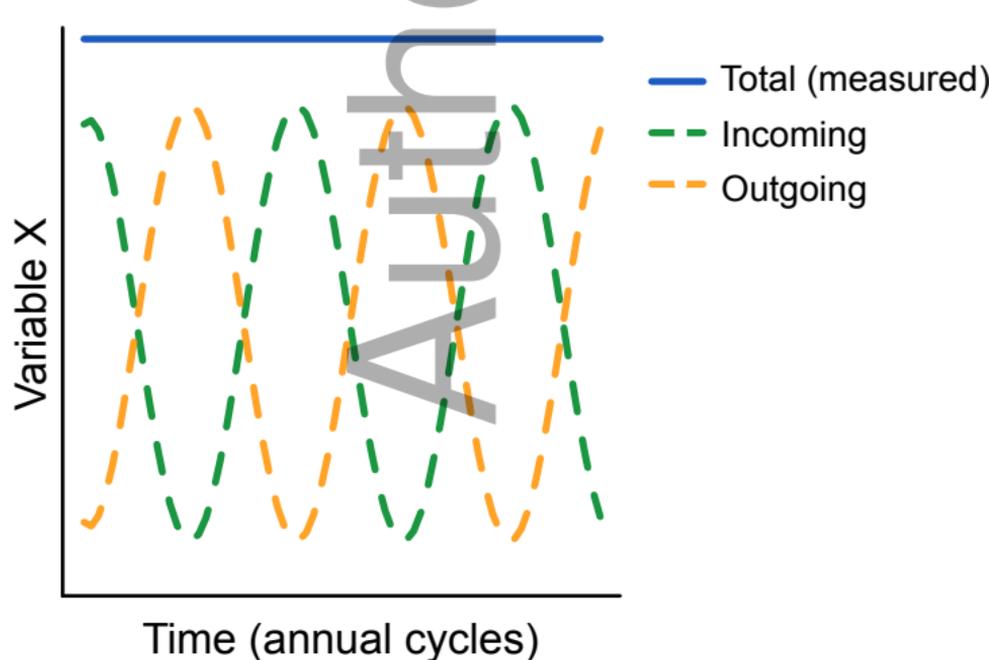
gcb-14759-11.pdf
(a) Example 1: Measured variable is the sum of multiple other variables with different temporal patterns

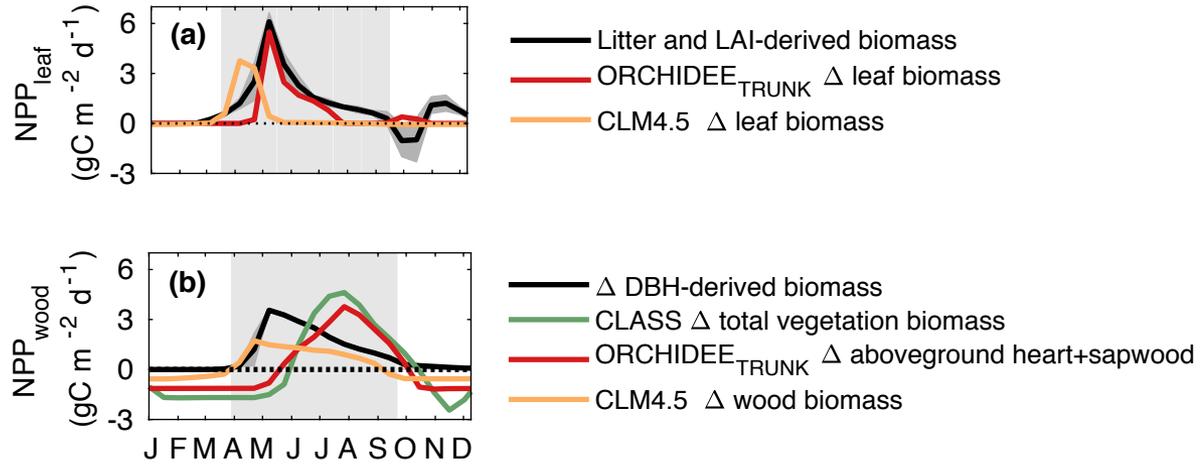


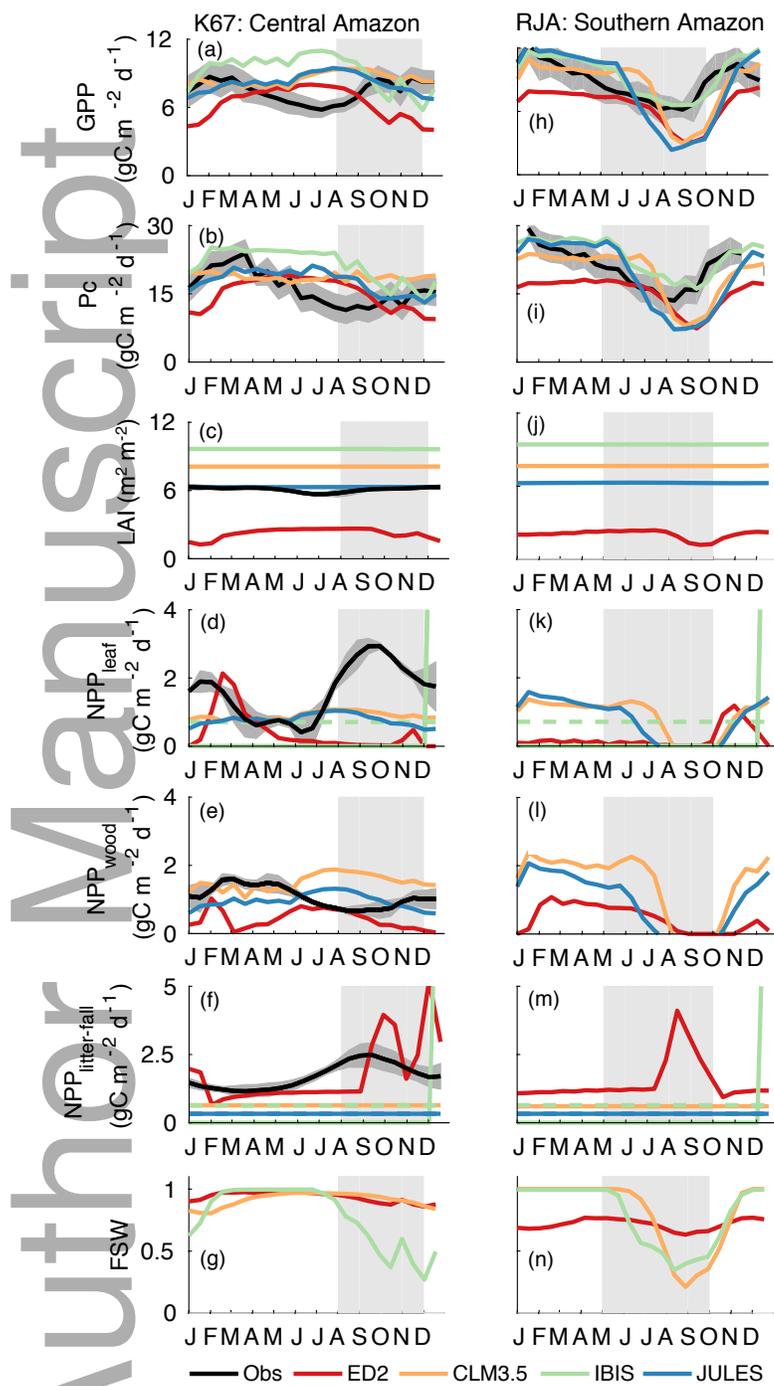
(b) Example 2: Measured variable is the sum of constant incoming and outgoing pools

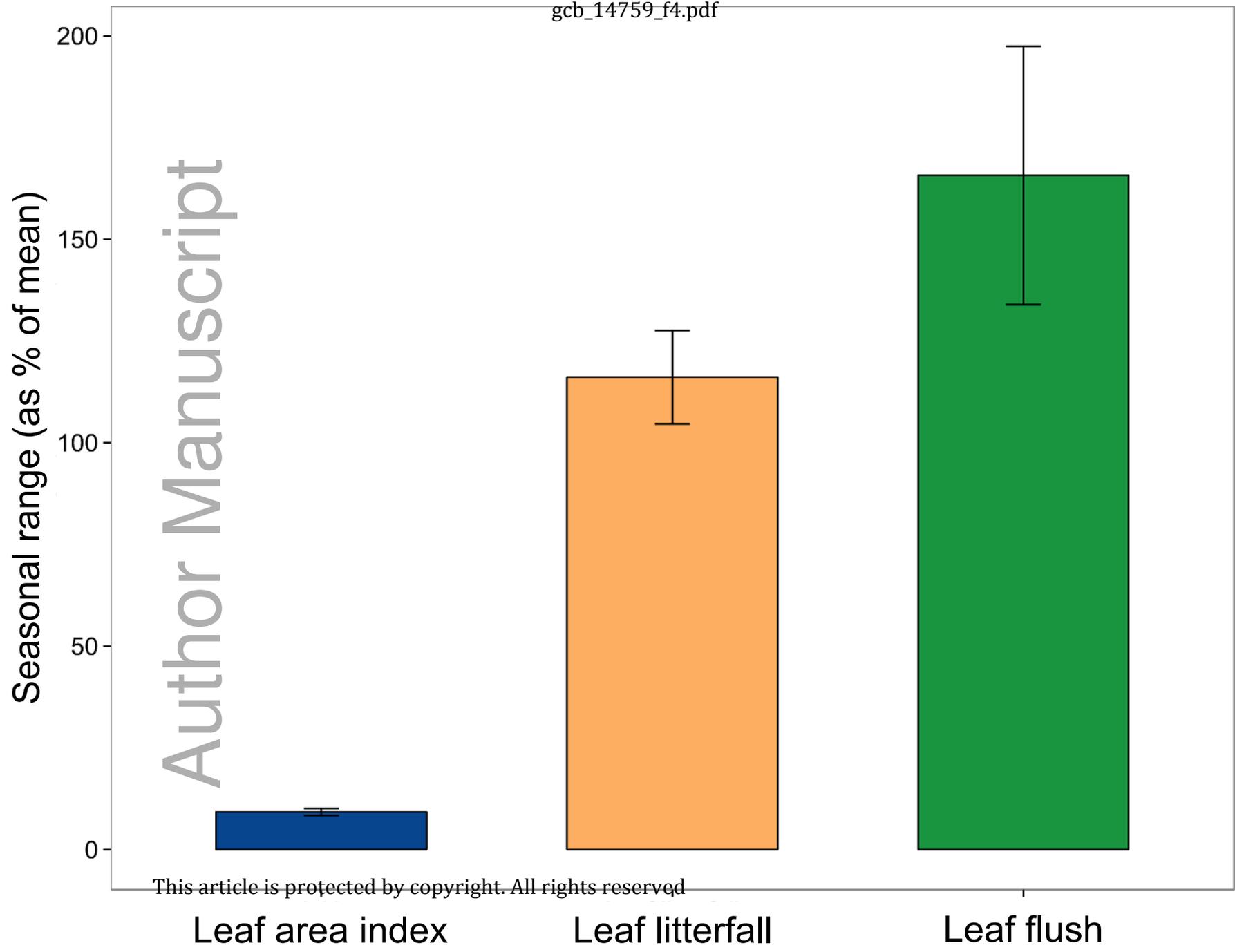


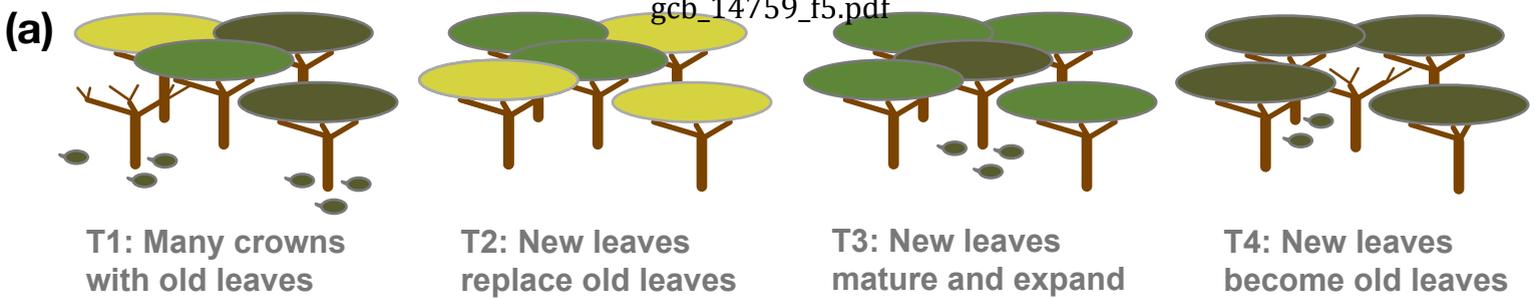
(c) Example 3: Measured variable is the sum of compensatory incoming and outgoing pools











 Crown with many young new leaves
 Crown with many mature new leaves
 Crown with many old leaves

