

Foster J.R. GROWTH AND MORTALITY RESPONSE TO DEFOLIATION

1 **Xylem traits and growth phenology predict growth and mortality response to defoliation in**
2 **temperate forests**

3

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23 **Abstract**

24 Defoliation outbreaks are biological disturbances that alter tree growth and mortality in
25 temperate forests. Trees respond to defoliation in many ways; some recover rapidly, while others
26 decline gradually or die. These differences may arise from species functional traits that constrain
27 growth such as xylem anatomy, growth phenology or non-structural carbohydrate (NSC) storage,
28 but this has not been shown. Although many studies address these phenomena, varied and
29 idiosyncratic measures limit our ability to generalize and predict defoliation responses across
30 species. I synthesized and translated published growth and mortality data into consistent
31 standardized variables suitable for numerical models. I analyzed data from 32 studies, including
32 16 tree species and 10 defoliator systems from North America and Eurasia, and quantitatively
33 compared responses to defoliation among species and tree functional groups using linear mixed-
34 effects models.

35 Relative growth decreased linearly or curvilinearly as defoliation stress accumulated across
36 species. Growth decreased by only 5-20% following 100% defoliation in ring-porous *Quercus*,
37 whereas growth of diffuse-porous hardwoods and conifers declined by 50-100%. Mortality
38 increased exponentially with defoliation, more rapidly for *Pinus* and diffuse-porous species than
39 for *Quercus* and *Abies*. Species-specific mixed models were best ($R^2c = 0.83-0.94$), yet
40 functional-group models lost little in terms of goodness-of-fit ($R^2c = 0.72-0.92$), providing useful
41 alternatives when species data is lacking. These responses are consistent with functional
42 differences in wood growth phenology and NSC storage. Ring-porous spring xylem growth
43 precedes budburst. Defoliators whose damage follows foliar development can only affect
44 development of later wood. Growth of diffuse-porous and coniferous species responds more
45 drastically, yet differences in NSC storage make them more vulnerable to mortality as stress
46 accumulates. Ring-porous species resist defoliation-related changes in growth and mortality

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47 more than diffuse-porous and coniferous species. These findings apply in general to disturbances
48 that cause spring defoliation and should be incorporated into forest vegetation models.

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51 **Introduction**

52 Tree and forest response to spring defoliation is a complex process. Trees lose photosynthetic
53 potential when they are defoliated early in the growing season, resulting in changes in growth.
54 They also die more often as defoliation stress interacts with other mortality factors. Yet trees are
55 long-lived, sessile organisms that must weather many disturbances over their lifetimes. In
56 adapting to this life history, they have become resilient to a wide range of climatic variation and
57 disturbance, including some amount of herbivory and defoliation. This adaptive resilience can
58 mask the effects of defoliation when disturbance years are observed in isolation, as some trees
59 show negligible response. Yet as stress accumulates over successive years of an outbreak,
60 changes in tree growth and mortality become more severe, consistent and interpretable
61 (MacLean 1980).

62 Tree responses to stress are increasingly viewed through the lens of inter-specific
63 differences in functional traits including leaf and wood growth phenology, xylem anatomy, and
64 non-structural carbohydrate (NSC) storage (Wiley & Helliker 2012, Panchen et al. 2014, Sevanto
65 et al. 2014). Ensembles of these traits are often linked. For example, deciduous species that leaf
66 out later tend to have larger xylem vessels than species that leaf out earlier (Lechowicz 1984,
67 Panchen et al. 2014), while species that store NSC primarily in leaves (conifers) tend to break
68 bud latest of all (Hoch et al. 2003, Michelot et al. 2012). These linkages may help explain
69 mechanisms of tree mortality under drought or other stresses (Sevanto et al. 2014), yet a
70 consensus on mortality mechanisms remains elusive (Wiley & Helliker 2012). Insect defoliation
71 is a periodic stressor of trees that is rarely brought to bear on ongoing discussions of carbon
72 starvation or hydraulic limitation hypotheses (Anderegg & Callaway 2012, Landhäusser &
73 Lieffers 2012). Yet defoliation stress is relatively straightforward: it directly limits the main

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74 source of C during a critical growing period. A better understanding of functional differences in
75 tree response to defoliation would provide insight into responses to distinct climate-related
76 stresses such as drought or late frost.

77 Extensive research quantifies growth and mortality responses to defoliation, yet it
78 remains difficult to generalize the results across species and ecosystems due to the wide variety
79 of data, models, and scales used by individual studies (Feicht et al. 1993, Hallet et al. 2006).
80 These disparities present a significant obstacle to the development of general models that
81 simulate how defoliation affects forest productivity. While extensive reviews exist for general
82 (Kulman 1971) and species-specific defoliation effects (Davidson et al. 1999; Jacquet et al.
83 2012), they stop short of quantitatively synthesizing results to compare defoliator systems (but
84 see MacLean 1980). Comparisons are complicated by the common use of categorical measures
85 of defoliation that differ. These measures may be defined by quantitative limits (e.g. low,
86 medium, and high defoliation classes may correspond to 0-30%, 30-60%, 60-100% defoliation,
87 or other limits), but they are typically reported and discussed categorically. These limitations
88 leave a gap in our understanding about forest response to large-scale, recurring insect disturbance
89 that contributes significant uncertainty to landscape- and global vegetation models.

90 We can reduce uncertainty in forest models by quantifying the different ways species
91 respond to stress and how those responses are linked to functional traits. We can also improve
92 how observations from field-based studies are scaled to geographic extents that are compatible
93 with vegetation models. Recent innovations using satellite data to quantify and map defoliation
94 create the potential to link spatially accurate estimates of disturbance stress with forest
95 characteristics and response (Townsend et al. 2012, Foster et al. 2013). In order to improve forest
96 models with realistic representations of defoliation severity, we need numerical relationships that

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97 link accumulated defoliation stress to growth suppression or mortality. Examples of such
98 empirical relationships exist for few defoliator systems (MacLean 1980; Alfaro et al. 1982). In
99 this analysis, I compare defoliation responses among several species from different tree
100 functional groups. I converted published data to standardized variables that lend themselves to
101 stand- and landscape-scale forest models and examined the data for significant trends,
102 relationships and differences among defoliator systems. Specifically, I sought studies that allow
103 quantification of both accumulated defoliation stress, which I define in a manner similar to
104 MacLean (1980) as the sum of annual defoliation over multiple years of an outbreak, and the
105 associated responses in terms of growth and mortality. I expected sensitivity to defoliation to
106 differ both by species and by functional groups defined by general tree-growth strategies.

107

108 **Materials and methods**

109 To test for generalizable relationships, I compiled research papers that reported defoliation as a
110 percentage of whole canopy foliage, or alternatively cumulative defoliation (defined as the sum
111 of annual defoliation over an outbreak or the product of average defoliation and outbreak
112 duration), as well as changes in growth and mortality as percentages (growth = % of average or
113 expected growth, cumulative mortality = % of population dying over a period of time, typically
114 5-10 years). Because repeated defoliation causes cumulative stress in trees, data from multiple
115 years of defoliation are of particular interest when modeling long-term effects (Blaise 1958;
116 MacLean 1980; Colbert & Fekedulegn 2001; Hennigar, MacLean & Norfolk 2007). Increasing
117 intensity over the duration of an outbreak can be captured by the summed, cumulative defoliation
118 in an objective, quantitative way (MacLean & Ostaff 1989). For papers where data were
119 presented in tables, graphs or text that could be converted to the described variables, I extracted,

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120 transformed and analyzed them in a consistent manner. I assigned categorical annual or
121 cumulative defoliation values to the numerical midpoint of the reported defoliation range (e.g. a
122 150-300% cumulative defoliation category, became 225% defoliation) (MacLean & Lidstone
123 1982). I treated the spruce budworm system (SBW) (*Choristoneura fumiferana*) as a special case
124 because cumulative defoliation is defined uniquely in this literature as an index of defoliation by
125 foliage age-classes. To retain comparison with existing published relationships, I did not rescale
126 these data to fit my definition of cumulative “total” canopy defoliation (e.g. simultaneous
127 defoliation of all foliage age-classes).

128 I selected results that reported the aggregate response of all tree canopy classes when
129 available, as many forest models do not track individual trees or their canopy status (Mladenoff
130 2004). When data were only reported for separate canopy classes (i.e. suppressed, intermediate,
131 or dominant) and sample sizes were available, I used weighted averages of all classes to estimate
132 aggregate stand response (Campbell & Valentine 1972). I did not distinguish among differences
133 in growth or mortality variables, such as mortality expressed as a percentage of basal area (BA)
134 or number of stems. My goal was to determine if average trends could be found in the extensive
135 empirical literature and whether trends would vary among tree species groups. I expected
136 considerable variability in both the predictor and response variables across studies, as the
137 methods of their estimation often lacked precision. Many papers only reported means of
138 cumulative defoliation categories, and relationships fit to mean values mask the variability
139 present in the raw, unreported data. The R^2 values reported from mean-only data do not represent
140 the variability expected from plot-level data, which would presumably result in lower R^2 .

141 I fit mortality response (%) to cumulative defoliation using a log transform to linearize
142 the relationship. I fit either linear or negative log-linear relationships between cumulative

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143 defoliation and growth (%) where appropriate. I report parameters and results in tables and back-
144 transformed models in figures with the raw data. When possible, I also fit models to annual
145 mortality rates, calculated by dividing raw reported mortality by the number of years over which
146 it had accumulated. When multiple datasets for similar species or defoliator systems existed, I
147 used mixed models (nlme package in R) to create combined models for annual rates that varied
148 intercept and slope as random effects by study and compared the results using Akaike
149 information criterion for small sample sizes (AICc).

150

151 **Results**

152 *Growth Response*

153 Average radial growth decreased linearly with accumulated defoliation stress for 9 of 16 data
154 sets that reported usable data, and followed a negative exponential relationship for the remainder
155 (Table 1, Figs. 1 and 2). Cumulative defoliation explained from 17 to 99% of the variance in
156 relative growth depending on the dataset, with typical R^2 values exceeding 0.80 (Table 1). The
157 rate of growth suppression, i.e., the slope parameter, tended to vary bimodally. More sensitive
158 tree species-defoliator systems exhibited a negative slope equal to a 50-100% suppression in
159 growth for a 100% increase in cumulative defoliation (Fig. 2a) (Kulman, Hodson & Duncan
160 1963; Alfaro & Shepherd 1991; Gross 1992; Erdle & MacLean 1999), while growth of other
161 species was reduced by only 5-20% over the same defoliation range (Figs. 1, 2 and 3, Table 1,
162 Appendix S1 in Supporting Information) (Baker 1941; Rose 1958; Rubtsov 1996; Colbert &
163 Fekedulegn 2001; Naidoo & Lechowicz 2001). Conifers including *Abies balsamea*, *Pinus*
164 *banksiana*, *P. pinaster*, *P. sylvestrus*, *Psuedotsuga menziesii*, *Larix laricina*, and diffuse-porous
165 *Populus* and *Acer* species composed the more responsive group, showing immediate, strong

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166 responses to a single year of defoliation. Species with slower, more moderate growth response
167 generated some radial growth even under severe defoliation, a trait characteristic of ring-porous
168 *Quercus* species, which have positive minimum growth thresholds due to their need to grow new
169 functional xylem cells every spring (Fig. 1). Trees with growth falling below these thresholds
170 would presumably reach a point from which they are unable to recover and subsequently leave
171 the pool of survivors. The lone deciduous conifer, *L. laricina*, responded less rapidly than *Pinus*
172 species, reducing growth at rates intermediate between examples of *P. tremuloides* and juvenile
173 *A. saccharum* (Appendix S1).

174 Negative curvilinear growth responses to defoliation were mostly associated with
175 immature trees (Fig. 2). These showed rapid early reductions in growth that were later
176 constrained by the theoretical minimum of zero (radial wood growth cannot be negative, though
177 stems will shrink under certain conditions (Stephens, Turner & Roo 1972; Wargo 1981; Alfaro et
178 al. 1982; Nichols 1988; Ostaff & Maclean 1995; MacLean & MacKinnon 1996)). The
179 curvilinear response is plausible in species that can survive many years without measurable
180 radial growth. Moreover, linear patterns become curvilinear if they approach lower bounds to
181 growth, and may simply represent a truncated view of the full relationship. This appears to be the
182 case for juvenile oaks that were manually defoliated by Wargo (1981) (Fig. 2a), whose growth
183 decreased more rapidly in a curvilinear fashion than mature, naturally defoliated oaks (Fig. 1).
184 Manually defoliated young *L. laricina* showed a similar curvilinear response (Fig. 2a). These
185 three patterns dominate the literature: negative curvilinear or linear growth responses with steep
186 or gradual slopes. This suggests consistent differences in the variability and range of growth
187 suppression among tree functional groups following defoliation stress.

188

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189 *Mortality*

190 I derived standardized cumulative defoliation and mortality data for 12 published studies
191 covering broad areas of North American and Eurasian temperate forest, several tree species, and
192 seven distinct spring defoliators of hardwoods, conifers or both (Table 2). Mortality increased
193 exponentially in all examples, approaching a sigmoid curve if severe enough, or observed long
194 enough, to saturate at 100% (MacLean 1980). This pattern was first observed by Blaise (1958)
195 for *Abies balsamea* mortality following spruce budworm defoliation (Appendix S2). Though the
196 available data show a consistent form for mortality relationships, the parameters varied for
197 different tree species and defoliator systems (Fig. 3, Table 2, Appendix S2 and S3). Cumulative
198 defoliation explained 90% of the variation in cumulative mortality of *Quercus* dominated forests
199 following *Lymantria dispar* L. (gypsy moth (GM)) outbreaks (Table 2, Feicht et al. 1993).
200 Mortality increased slowly at first, until cumulative defoliation reached about 150%, after which
201 mortality increased rapidly, approaching 100% (Baker 1941; Campbell & Valentine 1972; Feicht
202 et al. 1993; MacLean & Ebert 1999). A similar exponential increase was observed for single year
203 defoliation levels less than or equal to 100% (Table 2, Dobbertin & Brang 2005).

204 Alfaro et al. (1982) used a powered exponential relationship to explain over 99% of the
205 variance in mortality of Douglas fir (*Pseudotsuga mensiesii*) following a *Choristoneura*
206 *occidentalis* (western spruce budworm (WSBW)) outbreak (Table 2, Appendix S2). This
207 relationship is very similar to one derived here for *Abies balsamea* (balsam fir) mortality
208 following *Choristoneura fumiferana* (eastern spruce budworm (SBW)) defoliation from two
209 separate studies (Table 2, Fig. 3) (Blais 1958; Batzer 1973). These data agree with anecdotal
210 reports of mortality becoming severe following 3-4 years of complete defoliation (Kulman
211 1971), though these systems take much longer than deciduous ones to reach an equivalent

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212 amount of whole canopy defoliation (as opposed to defoliation of specific foliage age-classes
213 only). In particular, SBW outbreaks on *A. balsamea* take 10-12 years to produce equivalent
214 damage to entire canopies because they feed preferentially on current year foliage (MacLean
215 1980; MacLean & Ostaff 1989). Mortality in *A. balsamea* following *Lambdina fiscellaria*
216 *fiscellaria* (hemlock looper), a defoliator of all foliage age-classes, led to a more rapid increase
217 in mortality, closer to the range observed for *Pinus* species (Table 2, Appendix S2) (MacLean &
218 Ebert 1999).

219 When data from three studies of *Pinus* response, including mortality of young *P. strobus*
220 following GM defoliation and mature *P. banksiana* following *Choristoneura pinus pinus* (jack
221 pine budworm (JPBW)) defoliation (Baker 1941; Kulman et al. 1963) were combined (Fig. 3),
222 the best fit model shows mortality increasing more rapidly for defoliated *Pinus* than *Quercus*
223 species (Fig. 3, Appendix S2 and S3). Pines are typically thought to be capable of withstanding
224 only a few years of complete or severe defoliation, consistent with this rapid increase in
225 mortality (O'Neil 1962; Volney 1998).

226

227 *Differences in response models: species vs. functional group*

228 For cases where it was possible to formally compare mixed models (Appendix S3), models with
229 species-specific parameters always ranked higher than models that varied random effects based
230 on functional group. Species-specific random effects were best for all response models
231 regardless of whether intercepts, slopes, or both were varied (Appendix S3). Though species-
232 specific models represented the data best, functional group models lost little in terms of
233 goodness-of-fit. The variance explained by the best curvilinear growth response model by
234 functional group ($R^2_c = 0.72$) was not much lower than variance explained by the best species

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235 model ($R^2c=0.83$) (Appendix S3) (Nakagawa & Schielzeth 2013). Variance explained by the best
236 linear growth response models was similarly high for functional group ($R^2c=0.92$) as for species
237 ($R^2c=0.94$), and the best mortality functional group model ($R^2c=0.82$) lost little predictive power
238 compared to the best species model ($R^2c=0.87$). The similar predictive power of species and
239 functional group models suggests that functional group can be used as a surrogate to predict
240 growth and mortality response for tree species that lack data. It should be noted that mixed
241 models that vary only intercepts (*Quercus*, *Pinus*, Appendix S3) may be detecting differences
242 among the methods used by different studies to relativize growth responses against “normal”
243 growth, rather than meaningful biological differences among species.

244

245 **Discussion**

246 *Relationship of growth and mortality responses to phenology, wood anatomy and NSC storage*
247 Differences in growth strategies and wood anatomy among tree functional groups may help
248 explain the observed differences in shape and slope of the relationships reported here. For
249 example, oaks that survive several years of gypsy moth defoliation show a linear reduction in
250 growth of about 14-17% per 100% increase in defoliation. The best mixed models showed that
251 slopes did not differ significantly for analogous data collected in New England, Quebec, and
252 Russia (Baker 1941; Rubtsov 1996; Naidoo & Lechowicz 2001) (Appendix S3). Over the course
253 of an outbreak, radial growth was reduced by an average of 50-60% in these examples, but rarely
254 more. Temperate oaks are ring-porous species that must rely on large early wood vessels for
255 hydraulic transport. More than 90% of these vessels cavitate under freezing winter temperatures,
256 meaning that oaks’ hydraulic architecture will not function from one year to the next (Sperry et
257 al. 1994; Davis, Sperry & Hacke 1999). Temperate oaks overcome this limitation by storing

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258 excess starch reserves in sapwood over winter and drawing on them to build new xylem elements
259 the following spring (Barbaroux & Breda 2002). This early wood radial growth will actually
260 precede flushing of the leaves by two to six weeks, and is necessary to supply water to
261 developing foliage (Lechowicz 1984; Hacke & Sauter 1996; Suzuki, Yoda & Suzuki 1996,
262 Michelot et al. 2012). Accordingly, many *Quercus* species, and large vessel ring-porous species
263 in general, leaf-out later than other deciduous species (Lechowicz 1984, Panchen et al. 2014).
264 Growth phenology research using dendrometer bands has documented examples where 30% of
265 radial growth is completed before budburst, and 40% by the time tree canopies achieve
266 maximum LAI in June (Kulman et al. 1963; Hinckley & Lassoie 1981; Barbaroux & Breda
267 2002, Zweifel et al. 2006). Similarly, 50% of the total annual xylem was formed by June for
268 *Fraxinus excelsior*, another ring-porous species (Ladefoged 1952). As a consequence of these
269 traits, by the time larvae of spring defoliators are large enough to cause severe defoliation
270 damage, many oaks have already completed 30-40% of annual radial growth in the form of early
271 wood (Kozlowski 1969, Zweifel et al. 2006).

272 Xylem vessels are necessary for conductance to support leaves and photosynthesis,
273 creating a minimum cambial growth threshold for temperate, deciduous oaks that is typically 20-
274 40% of average radial growth. The curvilinear growth response of juvenile *Quercus* trees
275 defoliated by Wargo (1981) illustrates this well (Fig. 2a). Trees that are depleted of starch and
276 unable to regenerate a minimum vessel layer the following spring are likely to die and leave the
277 survivor pool. Studies of non-structural carbohydrate (NSC) storage also support this hypothesis,
278 though the mechanisms of the carbon starvation hypothesis remain in question (Hoch, Richter &
279 Korner 2003; Landhäusser & Lieffers 2012). Hoch et al. (2003) measured NSC allocation and
280 reserves for seven deciduous and three evergreen tree species and estimated that typical C

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281 reserves in deciduous species could regenerate the equivalent of four canopies of foliage. This
282 estimate agrees with anecdotal evidence that many trees die following three to four years of
283 complete defoliation and is consistent with curvilinear mortality rates (Fig. 3, Appendix S2).
284 Wargo (1981) measured starch reserves in juvenile *Q. velutina* and *Q. alba* as well as *Acer*
285 *saccharum* following three years of 100% artificial defoliation of June foliage. Starch dropped
286 curvilinearly to 11% and 0.2 % of average in *Q. alba* and *Q. velutina*, respectively. Starch in *A.*
287 *saccharum* dropped to 0%, leading to complete mortality. Diffuse-porous species such as *A.*
288 *saccharum* are less sensitive to limited radial growth. They retain multiple rings of functioning
289 xylem to meet hydraulic requirements. They may be more sensitive to rapid reductions in starch,
290 as they are less thrifty with NSC storage than *Quercus* species (Wargo 1981; Barbaroux & Breda
291 2002).

292 Diffuse-porous tree species from genera such as *Populus* (aspen), *Acer* (maples), and
293 *Fagus* (beech) demonstrate a different growth phenology than oaks. This phenology could
294 explain their wider range of radial growth response to defoliation. The smaller vessels in diffuse-
295 porous wood rarely cavitate and water transport is thus possible using existing xylem as soon as
296 spring conditions are suitable for budburst and shoot elongation (Lechowicz 1984; Davis et al.
297 1999). Diffuse-porous species typically utilize multiple annual rings for proper hydraulic
298 function. As a result, diffuse-porous species store less starch in sapwood, only needing enough to
299 generate a new set of foliage. These species leaf-out as early as possible when growing
300 conditions become suitable for early leaf development (Panchen et al. 2014), and the probability
301 of late frosts decreases (Barbaroux & Breda 2002). Diffuse-porous wood anatomy is often linked
302 to indeterminate growth habits, which allow species to continue to grow and respond to changing
303 conditions throughout the growing season (Kozłowski 1992). In comparison to ring-porous

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304 *Quercus*, diffuse-porous *Fagus* leaf-out earlier in the spring, do not initiate measurable radial
305 growth until two to seven weeks after budburst has occurred, and may achieve only 5-10% of
306 annual growth by the time canopies reach maximum LAI (Suzuki et al. 1996; Schmitt, Moller &
307 Eckstein 2000; Barbaroux & Breda 2002, Michelot et al. 2012)). In such cases, June herbivory
308 by defoliator larvae could suppress radial growth by up to 95%. The wider range in growth
309 response of diffuse-porous species leads to a steeper negative slope as defoliation stress
310 accumulates. At the same time, these strategies may improve survivability for some diffuse-
311 porous species, such as *Populus tremuloides*, by allowing trees to dedicate more available
312 photosynthate and NSC reserves to refoliation or chemical defense, rather than replenishing
313 reserves for future spring wood growth. The empirical evidence in the literature remains
314 equivocal on this topic. This review shows that defoliated young *A. saccharum* and mature *P.*
315 *tremuloides* do demonstrate a wider range in radial growth suppression than *Quercus* species
316 (Fig. 2); their growth was suppressed to below 20% of average over the observed range of
317 defoliation.

318 Conifers that retain foliage for multiple years employ yet another growth strategy that
319 contributes to a wider dynamic range of response to cumulative defoliation stress. Conifers that
320 retain two to three years of foliage (most *Pinus*) respond differently from those that retain four to
321 eight years of foliage age-classes (*Abies*, *Pseudotsuga*), as pines are generally more vulnerable to
322 their defoliators than firs. Conductive tissue in coniferous stemwood is made up of tracheids that
323 resist cavitation, a necessity for retention of green leaves throughout the winter dormant season
324 (Hinckley & Lassoie 1981; Tyree & Ewers 1991). Like diffuse-porous species, conifers are not
325 dependent on radial growth to renew xylem function and can survive periods with no radial
326 growth. This characteristic shows up as dropped rings in dendrochronological research. Unlike

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327 deciduous trees, conifers tend to utilize older foliage more than sapwood for NSC storage, and
328 rely on translocation from those stores to grow new foliage in the spring (Kozlowski 1992; Hoch
329 et al. 2003). New, current-year foliage is also responsible for a greater proportion of net
330 photosynthate production than older foliage. These characteristics mean radial growth response
331 to defoliation can range from 0-100%, and variation in preferential herbivory of old or new
332 foliage can produce linear or nonlinear relationships (Fig. 2b).

333 The simple, general relationships compiled here indicate that increasing defoliation stress
334 slows carbon accumulation in host species through destruction of foliar biomass and suppression
335 of radial stem growth. Productivity can be slowed at different rates, depending on the plasticity
336 and phenology of tree growth response and defoliator characteristics. Continuous defoliation also
337 increases tree mortality exponentially. Mortality rates increase most rapidly in *Pinus*, followed
338 by diffuse-porous genera such as *Acer* and *Populus*, then *Quercus*, and more slowly in *Abies* and
339 *Pseudotsuga* whose pests exhibit different feeding behavior. Nonlinear growth and mortality
340 responses can lead to extreme short-term losses in aboveground carbon. These relationships
341 allow us to more accurately quantify and model landscape-level effects on forest carbon
342 accumulation. This framework and approach for quantifying the accumulation of defoliation
343 stress and associated growth and mortality responses can be used in future empirical research to
344 facilitate comparison across more defoliator systems.

345

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351

352 **Data Accessibility**

353 - Defoliation, growth and mortality data extracted and transformed from published studies
354 will be archived on DRYAD, as well as associated R-scripts allowing replication of the
355 analysis.

356 - Appendix S1. Plots of derived growth data and back-transformed model fits by study:
357 uploaded as online supporting information

358 - Appendix S2. Plots of derived mortality data and back-transformed model fits by study:
359 uploaded as online supporting information

360 - Appendix S3. Model selection and parameter fits for mixed models of growth and
361 mortality data that could be compared within defoliator systems or across species groups:
362 uploaded as online supporting information

363

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504 **Figure Legends**

505

506 **Figure 1.** Growth response of *Quercus* species to *Lymantria dispar* (L.) (gypsy moth) defoliation
507 including *Quercus robur* (Rubstov 1996), *Q. velutina* (Baker 1941), *Q. rubra* (Wargo 1981), and
508 *Quercus alba* (Baker 1941, Wargo 1981). Lines show best fit mixed model (Appendix S3, Table
509 S3-1). The best combined *Quercus* model varied intercepts but not slopes.

510

511 **Figure 2.** Growth decreases curvilinearly to defoliation (a.) in *Populus tremuloides* (Rose 1958),
512 manually defoliated juvenile trees of *Acer saccharum*, *Q. alba*, and *Q. velutina* (Wargo 1981),
513 and *Larix laricina* (Ives and Nairn 1966). Linear growth responses of coniferous species (b.)
514 include steep declines in *Pinus banksiana*, *P. pinaster*, *P. sylvestrus* with slower declines in
515 *Pseudotsuga menziesii*, *Picea abies*, and *Abies balsamea*. The best fit mixed model (a., lines)
516 randomly varied slopes but not intercepts (Appendix S3, Table S3-1). Lines in (b.) show model
517 fits from Table 1 and the best mixed model for *Pinus* species that varied intercept, but not slope
518 (Appendix). *A. balsamea* relationship was published by Dobesberger 1998.

519

520 **Figure 3.** Cumulative mortality responses of example tree species to accumulated defoliation.
521 Mortality rates rise most quickly in *Pinus* (Baker 1941, Kulman et al. 1963, Gross 1992),
522 followed by diffuse-porous *Populus* (Mann et al. 2007), and then ring-porous *Quercus*
523 dominated forests (Feicht et al. 1993). Mortality in *Abies* appears to rise more slowly (Blais
524 1958, Batzer 1973), but defoliation in this system is defined differently as damage by foliage
525 age-class. Lines show model fits from Table 2. All plots can be found in Appendix S2.

526

527

528 **Table 1.** Models of relative tree growth response to cumulative defoliation. Input data were extracted and relativized from original
 529 studies to the same scale (details below).

530	531	532	533	534	535	536	537	538	539	540	541	542	543	544	545	546	547	548	549	550	551	552	553	554	555	556	557	558	559	560	
Location	Cum Defo.† Range (%)	Growth* Var.	Equation	<i>b</i>	<i>m</i>	R ²	Reference																								
<i>Lymantria dispar</i> (L.) defoliation of <i>Quercus robur</i>																															
Russia	0-300	RW	$y=mx+b$	80.00	-0.141	0.443	Rubstov (1996), Fig. 3																								
<i>Lymantria dispar</i> (L.) defoliation of <i>Q. coccinea</i> , <i>Q. alba</i> , and <i>Q. velutina</i>																															
Maine Massachusetts	0-400	Radial inc.	$y=mx+b$	96.177	-0.110	0.437	Baker (1941), Table 5																								
New England	0-800	Radial inc.	$y=mx+b$	70.553	-0.039	0.935	Baker (1941), Table 4																								
<i>Lymantria dispar</i> (L.) defoliation of <i>Q. alba</i> , and <i>Q. rubra</i>																															
New England	0-185	RW	$y=mx+b$	95.674	-0.278	0.877	Wargo (1981), Table 5.3																								
N. Temperate	0-800	all	$y=mx+b$	78.981	-0.100	0.254	Combined above																								
Quebec	NA	RW	$y=mx+b$	83.2	-0.165	0.730	Naidoo & Lechowicz (2001), Figure 6‡																								
Pennsylvania	0-170	RW index	$y=mx+b$	99.75	-0.168	0.168	Colbert & Fekedulegn (2001), Fig. 10‡																								
<i>Operophtera brumata</i> L. defoliation of <i>Q. rubra</i> and <i>Q. velutina</i>																															
Massachusetts	0-100	RW index	$y=mx+b$	120.2	-0.60	0.24	Simmons et al. (2014), Fig. 2‡																								

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561	Location	Cum. Growth* Defo.† Var. Range (%) (%)	Equation	<i>b</i>	<i>m</i>	R ²	Reference
565	<i>Malacosoma disstria</i> (Hubn.) defoliation of <i>Populus tremuloides</i>						
566	Ontario	0-100 Radial inc.	$y=be^{mx}$	4.346	-0.006¶	0.470	Rose (1958), Fig. 4
567	Manual defoliation of juvenile <i>Populus deltoides</i> clones						
568	Iowa	0-75 AGB inc.	$y=mx+b$	103.38	-0.442	0.613	Reichenbacker et al. (1996), Table 3
569	Manual defoliation of immature <i>Acer Saccharum</i>						
570	Eastern US	0-300 Radial inc.	$y=be^{mx}$	4.677	-0.015	0.984	Wargo (1981), Table 5-10c
571	Manual defoliation of immature <i>Quercus alba</i>						
572	Eastern US	0-300 Radial inc.	$y=be^{mx}$	4.572	-0.005	0.995	Wargo (1981), Table 5-10b
573	Manual defoliation of immature <i>Quercus velutina</i>						
574	Eastern US	0-300 Radial inc.	$y=be^{mx}$	4.382	-0.004 §	0.791	Wargo (1981), Table 5-10a
575	<i>Choristoneura pinus pinus</i> (Free) on <i>Pinus banksiana</i>						
576	N. America	0-94 Summerwood	$y=mx+b$	79.323	-0.826	0.998	Kulman et al. (1963), Table 4
577	<i>Thaumetopoea pityocampa</i> (Dennis & Schiff) defoliation of <i>Pinus pinaster</i> Ait.						
578	France	0-100 Radial inc.	$y=mx+b$	95.604	-0.874	0.983	Jacquet et al. (2013), Fig. 1
579	<i>Diprion pini</i> (Linneaus) defoliation on <i>Pinus sylvestrus</i>						

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594								
595	Finland	0-100	RW	$y=be^{mx}$	4.328	-0.029¶	0.975	Lyytkainen-Saarenmaa et al. (2002), Fig. 2
596								
597	N. Temperate	0-100	all	$y=mx+b$	82.666	-0.829	0.853	<i>Pinus</i> above combined
598								
599	<i>Orgyia pseudotsugata</i> (McDunnough) defoliation of <i>Psuedotsuga menziesii</i>							
600								
601	British Columbia	0-81	RW index	$y=mx+b$	88.080	-0.575	0.829	Alfaro & Shepherd (1991), Table 1
602								
603								
604	<i>Choristoneura fumiferana</i> defoliation on <i>Abies balsamea</i>							
605								
606	Newfoundland	0-100	Volume inc.	$y=mx+b$	100	-0.63	0.950	Dobesberger (1998), Equation 9‡
607								
608	General defoliation on <i>Picea abies</i>							
609								
610	Finland	0-100	Volume inc.	$y=mx+b$	116.31	-1.019	0.579	Salemaa & Jukola-Sulonen (1990), Fig. 3b
611								
612	<i>Gilpinia hercyniae</i> (Hartig) defoliation on <i>Picea sitchensis</i>							
613								
614	Wales	0-70	Volume inc.	$y=mx+b$	92.39	-0.600	0.570	Williams (2003), Tables 2 & 3
615								
616	Manual defoliation of young <i>Larix laricina</i>							
617								
618	Manitoba	0-300	Volume inc.	$y=be^{mx}$	5.146	-0.010	0.800	Ives & Nairn (1966), Fig. 1

619 * Growth is scaled from 0-100% of expected growth, either modeled, derived or observed in a control or prior to disturbance. Growth
 620 was measured by ring widths (RW), RW index, radial increment, volume increment, or summerwood width or some derivation of
 621 these. Please consult original articles for details.

622 † Cumulative defoliation is the sum of annual defoliation (0-100%) over the duration of a single outbreak (typically 1-5+ years).

623 ‡ Relationships published by original authors, included for comparison. When possible, formulae were rescaled to standardized ranges
 624 used here.

625 ¶ Probability that parameter is different from zero between 0.05 and 0.10. Probability of unmarked parameters < 0.05.

626 § Probability that parameter is different from zero > 0.10.

627 **Table 2.** Models of cumulative tree mortality or annual mortality rates derived from cumulative defoliation.
 628

629	Location	Cum Defo. Range (%)	Mort. Var. (%)	Annual Rate	Equation	b	m	R ²	Reference
633	<i>Lymantria dispar</i> (L.) defoliation of all species, <i>Quercus</i> dominant								
634									
635	Pennsylvania	0-365	BA		$y=e^{(mx+b)}$	1.704	0.008	0.901	Feicht et al. (1993), Table 2 & 3
636				yes	$(y+1)=e^{(mx+b)}$	0.521	0.006	0.876	Feicht et al. (1993), Table 2 & 3
637									
638	New England	0-263	stems		$y=e^{(mx+b)}$	1.495	0.010	0.574	Campbell & Valentine (1972), Tables 1,2,227-233
639				yes	$(y+1)=e^{(mx+b)}$	0.415§	0.007	0.662	Campbell & Valentine (1972), Tables 1,2,227-233
640									
641	New England	0-80	stems	yes	$y=e^{(mx+b)}$	1.611	0.010	0.773	Baker (1941), Table 1
642									
643	Pennsylvania	0-210	stems		$y=e^{(mx+b)}$	2.145	0.005	0.993	Herrick & Gansner (1987)
644				yes	$y=e^{(mx+b)}$	0.535	0.005	0.993	Herrick & Gansner (1987)
645									
646	N. America	0-365	all	yes	$(y+1)=e^{(mx+b)}$	0.547	0.006	0.839	Combined above, excluding Baker (1941)
647									
648	<i>Malacosoma disstria</i> (Hubn.) defoliation of <i>Populus tremuloides</i>								
649									
650	Ontario	0-300	stems		$y=e^{(mx+b)}$	2.135	0.008	0.918	Man et al. (2008), Fig. 4 & Table 1
651				yes	$y=e^{(mx+b)}$	0.583	0.007	0.981	Man et al. (2008), Fig. 4 & Table 1
652									
653	Minnesota	0-350	stems	yes	$(y+1)=e^{(mx+b)}$	2.806	0.007	0.667	Churchill et al. (1964), Table 1 and Text
654									
655	General defoliation of <i>Acer Saccharum</i>								
656									
657	N. America	0-95	BA	yes	$y=e^{(mx+b)}$	-0.784	0.045§	0.851§	Hallett et al. (2006), Fig. 4
658									
659									

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660	Location	Cum Defo. Range (%)	Mort. Var. (%)	Annual Rate	Equation	<i>b</i>	<i>m</i>	R ²	Reference
664	<i>Lymantria dispar</i> (L.) defoliation on <i>Acer rubrum</i>								
665	New England	0-263	stems		$y = e^{(mx+b)}$	2.202	0.006 ¶	0.457	Campbell & Valentine (1972), Tables 183-189
666				yes	$y = e^{(mx+b)}$	0.155 §	0.007	0.612	Campbell & Valentine (1972), Tables 183-189
667									
668	<i>Lymantria dispar</i> (L.) defoliation on <i>Pinus strobus</i>								
669									
670	New England	0-100	stems		$(y+1) = e^{(mx+b)}$	1.207 §	0.018 §	0.314	Baker (1941), Table 3
671				yes	$(y+1) = e^{(mx+b)}$	0.205 §	0.009	0.516	Baker (1941), Table 3
672									
673	<i>Choristoneura pinus pinus</i> (Free) on <i>Pinus banksiana</i> combined with above								
674									
675	N. America	0-138	stems		$(y+1) = e^{(mx+b)}$	1.552	0.014	0.418	Baker (1941), Kulman et al. (1963), Gross (1992)
676				Yes	$(y+1) = e^{(mx+b)}$	0.429 §	0.012	0.505	Baker (1941), Kulman et al. (1963), Gross (1992)
677									
678	<i>Choristoneura occidentalis</i> (Freeman) defoliation of <i>Psuedotsuga menziesii</i>								
679									
680	British Columbia	150-400	stems		$y = e^{(mx+b)}$	-1.163 §	0.016	0.955	Alfaro et al. (1982), Fig. 6
681				yes	$(y+1) = e^{(mx+b)}$	-3.424	0.016	0.955	
682									
683	<i>Lambdina fiscellaria fiscellaria</i> (Guen.) defoliation on <i>Abies balsamea</i>								
684									
685	New Brunswick	0-100	stems	yes	$y = e^{(mx+b)}$	-0.311 §	0.040	0.830	MacLean & Ebert (1999), Fig. 4
686		0-400	stems		$y = 10^{(mx+b)}$	0.647	0.006	0.790	MacLean & Ebert (1999), Fig. 6 ‡
687			volume	yes	$y = 10^{(mx+b)}$	0.647	0.006	0.817	MacLean & Ebert (1999), Fig. 6 ‡
688									
689	<i>Choristoneura fumiferana</i> defoliation on <i>Abies balsamea</i>								
690									
691	Ontario	0-400	stems		$(y+1) = e^{(mx+b)}$	-0.642	0.013	0.950	Blaise (1958), Fig. 2 & Table 1
692				yes	$(y+1) = e^{(mx+b)}$	-0.445	0.006	0.890	Blaise (1958), Fig. 2 & Table 1

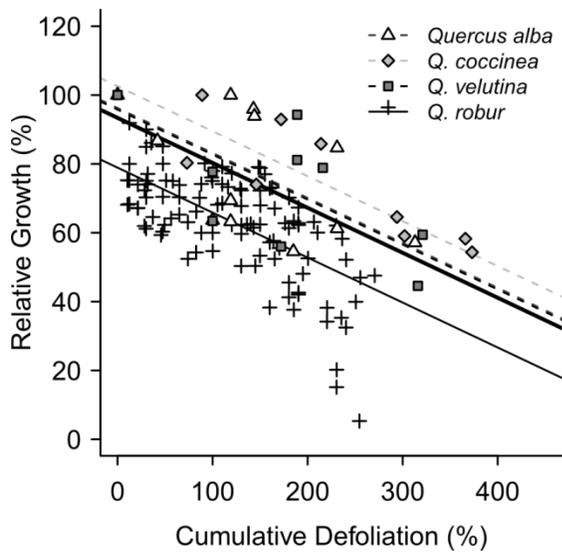
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693									
694	Minnesota	150-475	BA						
695				yes	$(y+1) = e^{(mx+b)}$	0.891	§ 0.007	0.847	Batzer (1973), Fig. 1
696					$(y+1) = e^{(mx+b)}$	-0.23	§ 0.006	0.831	Batzer (1973), Fig. 1
697	N. America	0-475	all						
698				yes	$(y+1) = e^{(mx+b)}$	-0.352	§ 0.011	0.914	Batzer (1973), Blaise (1958)
699					$(y+1) = e^{(mx+b)}$	-0.417	0.006	0.900	Batzer (1973), Blaise (1958)
700	All defoliation, all species								
701									
702	Switzerland	0-100	stems	yes	$y = e^{(mx+b)}$	-3.050	0.062	0.924	Dobbertin and Brang (2001), Fig. 1
703									

704 * Mortality ranges from 0-100% of the live tree population expressed as number of stems, basal area (BA), or volume.
 705 † Cumulative defoliation is the sum of defoliation (0-100%) over the duration of a single outbreak.
 706 ‡ Relationships published by original authors, included for comparison. When possible, formulae were rescaled to standardized ranges
 707 used here.
 708 ¶ Probability that parameter is different from zero between 0.05 and 0.10. Probability of unmarked parameters < 0.05.
 709 § Probability that parameter is different from zero > 0.

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711

712

713

714 **Figure 1.** Growth response of *Quercus* species to *Lymantria dispar* (L.) (gypsy moth) defoliation

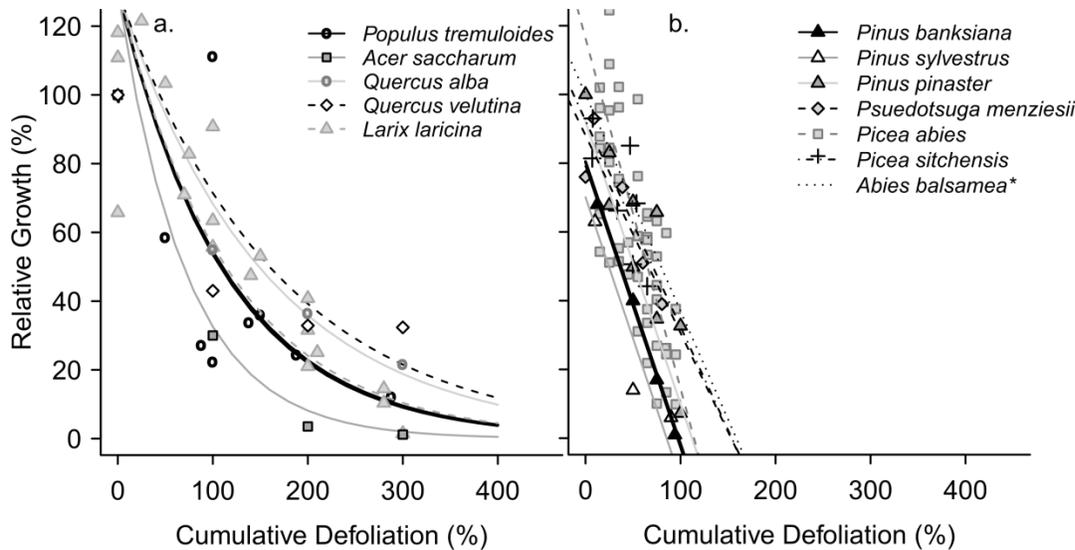
715 including *Quercus robur* (Rubstov 1996), *Q. velutina* (Baker 1941), *Q. rubra* (Wargo 1981), and

716 *Quercus alba* (Baker 1941, Wargo 1981). Lines show best fit mixed model (Appendix S3, Table

717 S3-1). The best combined *Quercus* model varied intercepts but not slopes.

718

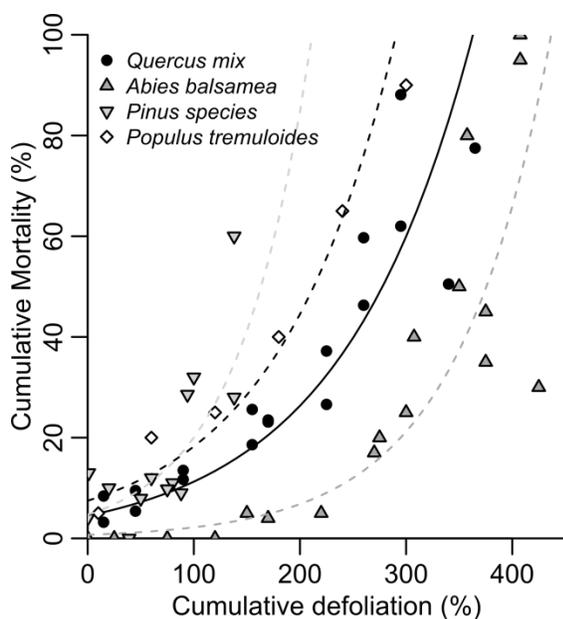
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719

720 **Figure 2.** Growth decreases curvilinearly in response to defoliation (a.) in *Populus tremuloides*
721 (Rose 1958), manually defoliated juvenile trees of *Acer saccharum*, *Q. alba*, and *Q. velutina*
722 (Wargo 1981), and *Larix laricina* (Ives and Nairn 1966). Growth of conifer species declined
723 linearly (b.) and included steep declines in *Pinus banksiana*, *P. pinaster*, *P. sylvestrus* with
724 slower declines in *Pseudotsuga menziesii*, *Picea abies*, and *Abies balsamea*. The best fit mixed
725 model in (a., lines) randomly varied slopes but not intercepts (Appendix S3, Table S3-1). Lines
726 in (b.) show model fits from Table 1 and the best mixed model for *Pinus* species that varied
727 intercept, but not slope (Appendix). *A. balsamea* relationship was published by Dobesberger
728 1998.

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729

730 **Figure 3.** Cumulative mortality increased exponentially in response to accumulated defoliation.

731 Mortality rates rise most quickly in *Pinus* (Baker 1941, Kulman et al. 1963, Gross 1992),

732 followed by diffuse-porous *Populus* (Mann et al. 2007), and then ring-porous *Quercus*

733 dominated forests (Feicht et al. 1993). Mortality in *Abies* appears to rise more slowly (Blais

734 1958, Batzer 1973), but defoliation in this system is defined differently as damage by foliage

735 age-class. Lines show model fits from Table 2. All plots can be found in Appendix S2.

736