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Title

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Permalink

<https://escholarship.org/uc/item/5ws238t1>

Journal

Tree physiology, 39(7)

ISSN

0829-318X

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Publication Date

2019-07-01

DOI

10.1093/treephys/tpz031

Peer reviewed

1 Fight or Flight? Potential tradeoffs between drought defense and reproduction in conifers

2

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10

11 Abstract

12 Plants frequently exhibit tradeoffs between reproduction and growth when resources are limited,
13 and often change these allocation patterns in response to stress. Shorter-lived plants such as
14 annuals tend to allocate relatively more resources toward reproduction when stressed, while
15 longer-lived plants tend to invest more heavily in survival and stress defense. However, severe
16 stress may affect the fitness implications of allocating relatively more resources to reproduction
17 versus stress defense. Increased drought intensity and duration have led to widespread mortality
18 events in coniferous forests. In this review, we ask how potential tradeoffs between reproduction
19 and survival influence the likelihood of drought-induced mortality and species persistence. We
20 propose that trees may exhibit what we call “fight or flight” behaviors under stress. “Fight”
21 behaviors involve greater resource allocation toward survival (e.g., growth, drought-resistant
22 xylem, and pest defense). “Flight” consists of higher relative allocation of resources to
23 reproduction, potentially increasing both offspring production and mortality risk for the adult.
24 We hypothesize that flight behaviors increase as drought stress escalates the likelihood of
25 mortality in a given location.

26

27 **Key Words:** carbon allocation, ecological tradeoffs, ecophysiology, hydraulic architecture, life
28 history traits, xylem anatomy

29 **Introduction**

30 Tradeoffs between reproduction and somatic investment have long been hypothesized
31 (Williams 1966), and evidence of such tradeoffs has frequently been observed. For instance,
32 perennial polycarpic plants often show a negative correlation between growth and reproduction
33 (Harper 1977). The principle of allocation (Levins 1968) suggests that the cost of one resource
34 sink can be quantified as the direct loss in potential allocation to a different sink. Different trait
35 combinations, given such tradeoffs, may be optimal under different environmental conditions.
36 For example, total lifetime fitness under non-stressful conditions may be positively correlated
37 with growth and survival that increase future reproductive success, or with current reproductive
38 effort at the expense of growth. Lifetime fitness is often maximized via intermediate investment
39 in both growth and current reproductive effort. As stress intensifies or is prolonged, however,
40 intermediate strategies may be less likely to maximize fitness as the overall pool of resources
41 that is being divided between growth and reproduction shrinks.

42 Tradeoffs between radial growth rate, tree hydraulic efficiency and safety are well
43 established in woody plants (Hacke et al. 2001, Pittermann et al. 2006b, Sperry et al. 2006), and
44 there is increasing evidence of tradeoffs between growth and reproduction under drought stress
45 (Woodward and Silsbee 1994, Climent et al. 2008, Hacket-Pain et al. 2017, Hacket-Pain et al.
46 2018). However, these tradeoffs are often explored independently. Our aim in this paper is to
47 briefly review what is known about these tradeoffs, and to present a conceptual model that
48 synthesizes the tradeoffs between growth and hydraulic safety, and between growth and
49 reproduction. Such a synthesis is necessary to move beyond simply predicting drought-induced
50 mortality, to better model what that drought-induced mortality means for long-term forest
51 dynamics including recruitment and overstory loss.

52 We propose that under extreme stress, trees may face a choice between two options.
53 They may "fight" by allocating more carbon (C) resources to survival-enhancing features such as
54 growth or defense at the expense of reproduction. Because perennial plants grow and reproduce
55 over many seasons, greater survival is usually likely to increase lifetime reproductive output
56 more than higher reproduction in any one year. Thus, this is the path one would expect trees to
57 follow under most circumstances. Alternatively, by allocating more resources to reproduction, or
58 not aborting reproductive structures already in various stages of production, they may increase
59 the probability that offspring will successfully germinate in favorable sites locally or in a
60 neighboring environment, achieving "flight." However, such a strategy could increase mortality
61 risk if the resources diverted from growth decrease stress defenses. This strategy is commonly
62 observed in annual plants (Wada and Takeno 2010, Suzuki et al. 2013) in which it often results
63 in early death or senescence.

64 We propose that perennial polycarpic plants might also exhibit a similar shift in
65 allocation if unfavorable conditions are sustained and the probability of adult mortality passes a
66 critical threshold, as has been occurring during increasingly intense and frequent drought
67 globally in recent years (Allen et al. 2015, Hartmann et al. 2018). For a tree, favoring growth and
68 survival over reproduction when under stress would usually be expected to maximize lifetime
69 fitness, as decades of potential future reproductive success become zero if a tree dies. However,
70 because fitness is zero if no seed is produced, and there may be a threshold level of stress that
71 will kill most trees in a population, under these conditions reproduction at the expense of
72 increased mortality risk may maximize lifetime fitness.

73 While multiple types of stressors could induce these shifts in allocation, we will focus
74 here on drought stress because closing stomata to reduce water loss (Tardieu and Simonneau

75 1998) decreases CO₂ uptake (Farquhar and Sharkey 1982) and availability of C for growth or
76 reproduction (McDowell et al. 2008). Recent work has attempted to parse mechanisms of
77 drought-induced mortality from both a physiological and C availability perspective (McDowell
78 et al. 2008, McDowell 2011, Kerhoulas and Kane 2012, Anderegg et al. 2012, Sala et al. 2012,
79 Anderegg and Anderegg 2013, Sevanto and Dickman 2015, Adams et al. 2017, Birami et al.
80 2018). However, there has been little synthesis across studies of drought-response physiology
81 and life history tradeoffs, and several prominent unanswered questions remain. These include:
82 How do climate and individual life history traits influence stress avoidance strategies?; Is there
83 an optimal strategy of resource use that allows for both survival and the highest chance of
84 successful reproduction under stressful conditions?; and what are the implications of tradeoffs
85 between survival and reproduction for species persistence under climate change? Answering
86 these questions requires a more robust scaling of mechanistic drought responses from the
87 individual cell to the whole tree with respect to both survival and reproduction.

88 In this paper, we focus on coniferous trees because they exhibit complex C dynamics,
89 with drought-killed trees demonstrating both altered C storage patterns and hydraulic failure. In
90 contrast, angiosperms primarily exhibit only hydraulic failure, with little evidence of C depletion
91 (Adams et al. 2017). In addition, unlike most angiosperm fruits, conifer cones can take up to
92 three years to mature following initiation (Mooney et al. 2011, Davi et al. 2016), potentially
93 making reproductive allocation more risky in highly variable and unpredictable environments.
94 However, though mechanisms involved may differ, similar tradeoffs are likely to occur in
95 angiosperm trees as well.

96 We first review current understanding of C allocation to growth, tradeoffs between
97 growth and hydraulic safety, and how drought modifies these allocation patterns. Tradeoffs

98 between growth and hydraulic safety are well studied (Xu et al. 2014, Venturas et al. 2017,
99 Barotto et al. 2018), but often only with respect to tree growth and survival. Here we place these
100 tradeoffs into a fitness context by reviewing the C budget implications of growth, hydraulic
101 safety, and the interaction of the two for reproductive capacity. Next, we discuss how drought
102 influences reproductive patterns, and evidence of tradeoffs between growth and reproduction.
103 We then present a new conceptual framework of C allocation under stress, and discuss both
104 evolutionary and ecological implications of tradeoffs among growth, reproduction, and defense
105 by distinguishing “fight” and “flight” strategies in stressed trees. Finally, we discuss
106 opportunities for research and synthesis across C budget studies, climate change experiments,
107 and analyses of tree physiology, with the aim of creating a more integrated understanding of tree
108 response to stress.

109

110 **Growth-survival relationships, as mediated by xylem hydraulic safety and carbon cost**

111 Growth is often used as a proxy for drought response in forest trees, with rapid or
112 prolonged periods of depressed growth suggesting an increased likelihood of mortality (Wyckoff
113 and Clark 2002, Das et al. 2007, Cailleret et al. 2017). However, in some trees, growth plasticity
114 under drought (Lloret et al. 2011) or overall slow growth (Moran et al. 2017) may in fact be a
115 drought resistance strategy. Growing less during drought and then rapidly increasing ring width
116 afterward may serve to conserve resources when water availability declines. This growth
117 plasticity may simply be a by-product of shifts in allocation of growth resources belowground
118 (Brunner et al. 2015, Hasibeder et al. 2015, Phillips et al. 2016), to carbohydrate storage pools
119 (Chapin et al. 1990, Luxmoore et al. 1995), or to non-woody tissues or osmo-regulatory
120 components (Gower et al. 1995). This relationship between growth plasticity and drought

121 tolerance is likely due to the complex interactions between growth and xylem anatomy during
122 times of C depletion.

123 Relationships among growth, xylem anatomy, and hydraulic safety are well established
124 (Sperry et al. 2003, Xu et al. 2014, Venturas et al. 2017, Barotto et al. 2018). Hydraulic failure –
125 breakage of the water column within xylem – can occur when air embolism blocks water flow
126 (Sperry et al. 1988, Cochard 2006, Barotto et al. 2018), or when water potentials within the
127 xylem become too negative and the xylem cell implodes (Hacke et al. 2001, Pittermann et al.
128 2006b). Drought increases the likelihood of either of these mechanisms of hydraulic failure by
129 decreasing water potentials within the soil and increasing the tension applied to the water column
130 along the soil-plant-atmosphere continuum (Hacke et al. 2000, Sperry et al. 2003).

131 Conifer resistance to hydraulic failure is a function of anatomy of xylem cells (tracheids)
132 and inter-tracheid pits (Hacke et al. 2001, Sperry 2003, Pittermann et al. 2006b, Sperry et al.
133 2006, Anderegg et al. 2015, Barotto et al. 2018). Trees with high resistance to hydraulic failure
134 often have thickened xylem cell walls, high wood densities, lower xylem cell diameter (D), and
135 lower inter-tracheid pit area than those that are less resistant (Hacke et al. 2001, Pittermann et al.
136 2006a, Pittermann et al. 2006b, Guet et al. 2015, Barotto et al. 2018). However, increases in wall
137 thickness (t) and wood density represent multiple tradeoffs. First, trees with a high ratio of cell
138 wall thickness to diameter (t/D) often have low hydraulic efficiency, as small xylem cells
139 transport less water than larger cells (Hacke et al. 2001, Pittermann et al. 2006b). Additionally,
140 thickened xylem cell walls have a higher C cost than thinner walls, potentially leading to
141 tradeoffs among hydraulic safety and other potential C sinks such as radial growth (Figure 1).

142 Tracheid walls are mostly composed of cellulose and hemicellulose (primary cell wall)
143 and lignin (secondary wall). In conifers, radial growth is often positively correlated with tracheid

144 abundance and size, with larger ring widths being associated with more numerous and thinner-
145 walled tracheids (Xu et al. 2014, Cuny et al. 2014). Tracheid wall thickness is positively
146 correlated with lignin concentrations (Gindl 2001). Lignin contains, on average, 30% more
147 energy (in the form of C) than cellulose (White 2007, Novaes et al. 2010). High negative
148 correlations have been shown between total tree biomass and lignin concentrations (Novaes et al.
149 2010), demonstrating that decreased radial growth is often associated with increased relative
150 lignin (and thus increased C cost) per unit volume of wood. Lignin concentration in
151 gymnosperms is negatively correlated with Ψ_{50} (the water potential at which 50% of
152 conductivity is lost, Figure 2). This is likely due to tracheid wall reinforcement, but there is also
153 mixed evidence of lignin deposition into the various components of inter-tracheid pit membranes
154 that may alter embolism resistance (Pereira et al. 2018). While the role of lignin in reducing
155 likelihood of cavitation must be further explored, this data demonstrates that constructing
156 drought-resistant xylem is lignin intensive. Thus, the tradeoffs among radial growth, xylem
157 hydraulic safety, hydraulic efficiency, and the C cost of all three of these components show that
158 growth and “type” of growth (i.e., high or low radial growth versus hydraulic safety) are only
159 loosely dependent, and may be independent under drought stress. For example, two trees may
160 grow rings of equal width, but with significantly different hydraulic safety and relative C
161 investment; radial growth and hydraulic safety do not necessarily constrain each other, but may
162 if resources are depleted.

163 The C costs of growth-related structures are further exacerbated by the multiple
164 interactive stresses often placed on trees during drought. In many coniferous forests, for
165 example, outbreaks of wood-boring insects and other pests coincide with drought stress due to
166 weakened pest defenses and ideal conditions for pest proliferation (Hicke et al. 2016). Both

167 chemical and physical defenses to pests represent a significant C cost (Franceschi et al. 2005).
168 The quantity of resin ducts, which transport C-based defensive compounds, and the ratio of resin
169 ducts to xylem cells, are both positively correlated with survival of bark beetle attack in conifers
170 (Kane and Kolb 2010, Ferrenberg et al. 2014). Tree growth and resin duct properties (including
171 duct density) are also positively correlated, suggesting that conditions conducive to growth are
172 also conducive to increased defenses (Kane and Kolb 2010, Ferrenberg et al. 2014), likely due to
173 high availability of resources, including C. While resin duct formation tends to decrease under
174 drought stress (Slack et al. 2017), allocation of resources to resin ducts can rise when trees are
175 deprived of phosphorus (Ferrenberg et al. 2015), showing that different stresses can induce
176 different changes in resource allocation to pest defense. Thus a tradeoff exists between stress
177 defense (both drought and pest) and other resource sink demands, such as growth or
178 reproduction.

179

180 **Mast seeding and carbon costs**

181 Average construction costs of seed vary and are not always significantly different from
182 leaf and stem tissue, but maximum seed construction costs are often much higher than other
183 tissues (Poorter et al. 2006). Reproductive structures can consume 6-10% of annual net canopy
184 photosynthesis (Gower et al. 1995). Immature conifer cones can photosynthesize, but McDowell
185 et al. (2000) reported that cone photosynthesis in *Pseudotsuga menziesii* can only provide about
186 27% of the C cost of cone production. The remaining C for cone formation must come from
187 current photosynthetic activity or via drawing on C stores. Some data suggest potential C-
188 limitation of reproduction. For instance, CO₂ fertilization of *P. taeda* induces larger cones and
189 earlier seed production relative to tree size than under ambient conditions (Way et al. 2010).

190 Similarly, *P. taeda* trees exposed to elevated CO₂ produced three times as many cones and were
191 twice as likely to be reproductively mature as trees of the same size grown in ambient conditions
192 (LaDeau and Clark 2001).

193 Masting, the production of large seed crops in synchrony across a population at semi-
194 regular intervals, is a common reproductive strategy in trees (Kelly and Sork 2002). The
195 advantages of this strategy are twofold. First, synchronous flowering/pollen production can
196 increase successful ovule fertilization (Mooney et al. 2011, Rapp et al. 2013, Koenig et al. 2015,
197 Bogdziewicz et al. 2017), perhaps especially in species that rely on wind to transport their pollen
198 rather than the more directed dispersal services of animal pollinators. Second, synchronous seed
199 production can satiate predators, reducing the proportion of seeds that get damaged or eaten
200 (Mooney et al. 2011, Koenig et al. 2015). However, these reproductive flushes represent a
201 significant potential resource expenditure at particular time intervals (Hackett-Pain et al. 2015,
202 Pearse et al. 2016). Studying trees with this reproductive pattern allows direct measurement of
203 plant status and resource investment before, during, and after a mast (Herrera et al. 1998).

204 Weather may affect particular stages of reproduction in different ways (Figure 3, Table
205 1). For instance, in species where the source of C for reproduction has been studied, spring
206 reproductive structures (flower or immature female/pollen cones) tend to be built with stored C,
207 while most of the C for developing fruits or cones comes from current-year assimilation (Hoch et
208 al. 2003). Thus, weather conditions favorable for photosynthesis (relatively moist, moderately
209 warm) during the seed development period are likely to be associated with larger seed crops
210 (Keyes and González 2015, Guo et al. 2016b). However, the amount, synchrony, and
211 effectiveness of pollen dispersal, which sets the stage for fruit/cone development, is often
212 favored by dry, warm, or dry and warm spring conditions (Koenig et al. 2015, Pearse et al. 2016,

213 Bogdziewicz et al. 2017, Gallego Zamorano et al. 2018). The pollen dispersal stage in turn
214 depends on the development of flower/cone primordia and the meiosis that produces the
215 precursors of ovules and pollen. This is often favored by warm conditions in the previous spring
216 and summer (Smaill et al. 2011, Bogdziewicz et al. 2017, Gallego Zamorano et al. 2018), though
217 that is not universal (Mooney et al. 2011), and may depend on whether the species is more
218 limited by cold or drought. Finally, in at least some species, the year prior to primordia formation
219 seems to be important for "resource priming" (Buechling et al. 2016), and the uptake of nitrogen
220 (N) and other nutrients incorporated at this stage is often favored by moist, cool, or moist and
221 cool conditions (Mooney et al. 2011, Smaill et al. 2011).

222 There are tradeoffs evident in resource allocation to different stages of reproduction. In
223 pines, which develop cones over two to three years, the cone maturation period that will result in
224 seed dispersal in the fall of year one overlaps with two years of cone primordia initiation and one
225 year of pollen production and dispersal (Figure 3). Any resources devoted to one of these stages
226 cannot be allocated to the others, likely resulting in masting periods that approximate a 3 year
227 cycle (Guo et al. 2016b). Even in trees with a shorter seed development period, years of high
228 seed production tend to be followed by years of low seed production, even if favorable weather
229 conditions persist. This may account for patterns such as warm spring weather in the year of
230 flowering and two years prior being positively associated with seed production, but warm spring
231 weather one year prior being negatively associated with seed production (Keyes and González
232 2015, Pearse et al. 2016, Gallego Zamorano et al. 2018).

233 There is mixed evidence for tradeoffs among growth and reproduction during drought
234 (Table 1). Tree growth is often decreased both during mast years and one year following masts
235 (Hackett-Pain et al. 2017, Hackett-Pain et al. 2018). While positive correlations between growth

236 and reproduction in non-masting years have been observed in *Pinus halepensis* (Santos et al.
237 2010, Ayari et al. 2012, Ayari and Khouja 2014), *P. pinaster* (Santos et al. 2010), *P. banksiana*
238 (Despland and Houle 1997), and *Abies sachinensis* (Hisamoto and Goto 2017), none of these
239 studies explicitly assessed the growth-reproduction relationship in mast years versus non-mast
240 years. Woodward and Silsbee (1994) found that both *A. lasiocarpa* and *Tsuga mertensiana*
241 showed positive correlations between growth and reproduction overall, but that large cone crops
242 (i.e., mast years) were associated with decreased radial growth. Koenig and Knops (1998) found
243 negative correlations between vegetative growth and reproductive output over multiple years in
244 both *Picea* and *Pinus* spp., and argue that this is direct evidence of a “switch” in C allocation
245 between mast events. Eis et al. (1965) found that ring widths in *P. menziesii* over a 28-year
246 period were only depressed during years of large cone crop production. Finally, a recent
247 experimental study found that pines from which developing cones were removed grew
248 marginally more immediately after the treatment, and also produced 70% more cones the year
249 after, compared to control trees (Santos-del-Blanco et al. 2012). This suggests that resources may
250 be mostly or entirely allocated to reproduction but re-allocated following cone removal.

251

252 **Drought impacts on reproduction**

253 Reproductive response of conifers to drought stress varies widely (Table 1). Direct
254 evidence of drought-induced reproduction in conifers is mixed, and often difficult to directly
255 assess (Davi et al. 2016). In part, this may be because, as mentioned above, climatic conditions
256 can influence reproductive allocation during cone initiation, growth, and maturation differently.
257 Consistent with the favorable impacts of dry conditions on pollination, several studies in conifers
258 have found either negative correlations between initial male and female cone production and

259 precipitation (Roland et al. 2014), or positive associations between water stress and initial female
260 cone production (Greenwood 1981, Riemenschneider 1985). On the other hand, wet years are
261 better for C assimilation, and have been found to be positively associated with the initiation of
262 cone primordia (Mooney et al. 2011) or the development of fertilized cones (Roland et al. 2014,
263 Keyes and González 2015, Guo et al. 2016b).

264 Because cone production is usually a multi-year process, a switch in C allocation toward
265 greater relative investment in growth than reproduction during a low-resource year would likely
266 result in abortion of currently developing cones. Cone abortion in conifers does appear to be
267 higher in subdominant trees than dominant trees under ambient conditions (Goubitz et al. 2002).
268 This may be the result of decreased CO₂ under light limitation (Berdanier and Clark 2016),
269 leading to abortion of cones whose development cannot be safely supported. Thus, one potential
270 direct indicator of altering C allocation to reproduction or growth under drought stress would be
271 drought-induced increases in cone abortion rates, as trees shunt resources from cone production
272 back into growth, drought defense, or pest defense.

273

274 **Fight or Flight**

275 *Tradeoffs between growth, defenses, and reproduction*

276 If there are tradeoffs between growth and hydraulic safety, as well as between growth and
277 reproduction, the C depletion experienced by trees under drought stress may further exacerbate
278 the impacts of these tradeoffs. This may lead to one strategy (i.e. allocation to hydraulic safety,
279 allocation to rapid radial growth, allocation to storage, or allocation to reproduction) becoming
280 dominant. If trees exhibit significant tradeoffs between xylem construction and reproductive
281 patterns, they may be displaying variations on classic “fight or flight” behaviors (Cannon 1915).

282 If a stressed tree invests more of an available resource into defenses (against drought, pests, or
283 competition) at the xylem anatomy, growth, or C storage levels, then this may be considered a
284 “fight” behavior. Fight behaviors include numerous actions currently categorized under such
285 terms as drought avoidance, drought tolerance, and drought resilience (Heschel and Riginos
286 2005, Lloret et al. 2011, Moran et al. 2017). Fight behaviors may increase likelihood of survival,
287 potentially at the expense of reproductive success in the current or next year but allowing for
288 later reproduction. If a tree instead invests more available resources into reproduction, either
289 through maintenance of investment in previously initiated cones or through new cone initiation,
290 this may be considered a “flight” behavior. Such a reproductive pulse could increase the risk of
291 tree death under low resource conditions, but may also maximize lifetime fitness if mortality risk
292 is already high and investment in reproduction increases the probability that offspring will reach
293 suitable sites for establishment.

294 No current conceptual models of C allocation partition growth apportionment into sub-
295 categories, such as hydraulic architecture versus radial growth. While radial growth produces
296 new xylem, the anatomy of the xylem that makes up that radial growth can vary widely from
297 year-to-year or tree-to-tree, affecting hydraulic safety. Few models of C allocation distinguish
298 “types” of radial growth, such as the C cost of high radial growth with low wood density (and
299 associated low hydraulic safety) versus the cost of low radial growth with high wood density.
300 Such partitioning is important to fully understand the fitness implications of C allocation. Low
301 stem radial growth is often predictive of mortality (Das et al. 2007), but lack of growth cannot be
302 deemed drought intolerance if the tree is re-partitioning available resources to other “fight”
303 behaviors that increase survival probabilities (e.g., decreased growth as a function of increased
304 tracheid lignification, increased defensive chemicals, or increased root growth). Tradeoffs may

305 occur not only between reproduction and growth, but also between growth of different tissues
306 (i.e., stem, leaf, or root), and between different components of tissue growth, such as tracheid
307 widening versus thickening.

308

309 *Physiological mechanisms of tradeoffs*

310 The density of sapwood, the zone of active xylem transport in a tree stem, is negatively
311 correlated with whole plant hydraulic conductance (K ; Mencuccini (2003) and xylem cell
312 enlargement (Cuny et al. 2014), and positively correlated with tracheid wall thickness
313 (Pittermann et al. 2006b). High K is also associated with high photosynthetic capacity and
314 general plant vigor (Mencuccini 2003), and leaf area often scales linearly with sapwood
315 conductive area (Luxmoore et al. 1995, Trugman et al. 2018). Thus, we can consider tracheid
316 diameter (which is positively correlated with K), wall thickness, and number—in terms of their
317 effects on whole plant hydraulics, stem sapwood growth, and C acquisition at the leaf level—and
318 further parse the responses of these components to drought.

319 Under drought, high K does not always increase survival. In fact, high K relative to
320 hydraulic safety (i.e., low xylem wall thickness or inter-tracheid pit resistance to cavitation) may
321 increase risk of mortality (Pittermann et al. 2006b). Drought stress will likely lead to increased
322 investment in wall thickening in newly grown tracheids, and to decreases in K . Turgor-limited
323 cell expansion provides a mechanism for this shift. Cellular radial growth is constrained by the
324 amount of water present, which drives tracheid cell enlargement prior to wall lignification and
325 cell death (Woodruff et al. 2004). Cell lumen diameter is highly dependent on how long turgor
326 can be maintained; the longer the expansion phase, the larger the lumen diameters and the
327 smaller the t/D of the cell (Anfodillo et al. 2012). If a plant is drought stressed, cell turgor tends

328 to be reduced, leading to drought-induced decreases in new xylem cell diameters and a relative
329 increase in wall thickness (Cuny et al. 2014). This would result in a decrease in K , which may
330 signal defoliation and thus reduced photosynthetic capacity. Further, a decrease in K via
331 decreased tracheid lumen diameters and increased wall thickness would result in an increase in
332 the relative C cost per unit volume of wood produced. Thus, the relationship between K ,
333 photosynthetic capacity, and hydraulic safety represents a positive feedback loop; drought would
334 induce smaller tracheids with a higher hydraulic safety and higher relative C cost, which is
335 further exacerbated by decreased C uptake potential.

336 Unlike growth, which contains further allocation tradeoffs, reproduction represents only
337 one significant tradeoff to the tree - the potential net loss of resources to reproduction from all
338 other processes. However, as mentioned above, there may be tradeoffs in allocation between
339 developing fertilized cones and cone primordia that results in negative correlations of current
340 year seed production with reproduction in the year or two prior. Additionally, reproduction may
341 reduce photosynthetic capacity, as cones take up branch area that may normally be covered in
342 needle tissue (Luxmoore et al. 1995). However, surrounding photosynthetic tissues may
343 compensate for decreased leaf area, at least to some degree. Carbon assimilation dynamics are
344 increasingly being shown to be sink-controlled (Luxmoore et al. 1995, Sala et al. 2012, Hayat et
345 al. 2017). That is, as C demand at sinks increases, photosynthesis may be up-regulated. Yet, in
346 the context of drought, if C sink demand increases photosynthetic activity, we may expect
347 increased water loss due to increased stomatal conductance. This would increase the likelihood
348 of hydraulic failure or lead to stomatal closure to mitigate water loss, counter-acting any
349 potential cone-driven increases in C assimilation via photosynthesis.

350

351 *Conceptual model of C allocation tradeoffs*

352 By incorporating these various components of growth—radial growth, xylem anatomy,
353 and the tradeoffs between hydraulic safety and hydraulic capacity—into a new conceptual model
354 of C allocation, we can examine the implications of multiple tradeoffs in the C allocation
355 pathway for masting conifer species in drought-prone environments (Figure 4). Under stressful
356 conditions, we would expect the uppermost tradeoff in the allocation hierarchy to be
357 exacerbated, if the C cost of both growth and reproduction is too high for the stressed tree. As
358 discussed above, we would expect conifers in most situations to exhibit “fight” responses to
359 stress (Figure 4A), with increased relative investment in components of growth, including
360 induced defenses. This will maximize their potential to survive the stress and reproduce in
361 subsequent years, even if current year reproduction is suppressed. However, if drought is
362 prolonged or reaches an intensity threshold beyond which survival is unlikely, flight may be
363 more beneficial.

364 Two potential fight responses are possible if direct tradeoffs exist between C allocation to
365 belowground versus aboveground growth (Figure 4A). The first possibility is investment
366 primarily in root growth, which could enable trees to reduce drought stress by accessing more
367 water. Some studies in seedlings have found increased root allocation early in drought, though
368 roots can die as drought intensifies or lengthens (Brunner et al. 2015). There is some evidence of
369 enhanced root non-structural carbohydrate (NSC) allocation during drought in many taxa
370 (Hagedorn et al. 2016, Kannenberg et al. 2017, Piper et al. 2017), though other studies have
371 found no significant change in C mobilization belowground (Kerhoulas and Kane 2012, Blessing
372 et al. 2015), or decreased root NSC and increased stem NSC (Birami et al. 2018, Li et al. 2018).
373 Changes in strategy from passive to active root C storage instead of growth may represent in-

374 season switches in C allocation that serve to build up C reserves and shorten stress recovery time
375 (Hagedorn et al. 2016).

376 The second possible C allocation pathway associated with a fight response would be to
377 aboveground growth or chemical pest defenses. Aboveground C allocation can result in either
378 increased radial growth, increased hydraulic safety, or increased chemical defenses. Turgor-
379 limited cell expansion would be expected to lead to decreased tracheid diameter and increased
380 relative wall thickness. Maximizing radial growth may increase susceptibility to hydraulic
381 failure, but will also increase competitive ability, particularly if a tree survives the drought.
382 However, growing small rings in order to maintain hydraulic safety does not preclude a tree from
383 maintaining a large sapwood area and post-drought competitive ability. Theoretically, if a
384 “fighting” tree does not maximize growth increment but instead grows larger numbers of smaller
385 tracheids, K per unit area of wood (and associated canopy leaf area) can be maintained with little
386 change in hydraulic safety, but at a higher C cost than small rings or large rings with large
387 tracheids. Such a pattern has been demonstrated in nature; *Picea crassifolia* grew larger rings
388 when more numerous smaller tracheids were produced and smaller rings were associated with
389 less numerous larger tracheids (Xu et al. 2014). While this study did not directly assess C or
390 lignin content of measured rings, we would expect these larger, tracheid-dense rings to be more
391 C-expensive than the smaller rings, demonstrating fight behavior. Finally, drought stress may
392 induce increased production of C-rich chemical defenses against pests that attack drought-
393 weakened trees, such as terpenoids and phenolic compounds (Turtola et al. 2003), or resin
394 (Franceschi et al. 2005). The production of these chemicals may preclude other C-expensive
395 processes, thus representing fight behavior.

396 Flight responses would be demonstrated by maintained or increased relative allocation to
397 reproduction (Figure 4B). Due to the relationship between growth, tracheid diameter, and
398 sapwood conductance (Mencuccini 2003, Pittermann et al. 2006b), if a switch in C allocation
399 leads to decreased growth and increased reproduction, we would expect a decrease in K and total
400 photosynthetic capacity in subsequent years relative to average climatic conditions, as well as
401 decreased C availability for pest defenses. Thus, a stress-induced mast is likely only a viable
402 strategy if risk of mortality is already high or if tree resource pools are sufficient. Another
403 potential flight response in conifers would simply be continued development during drought
404 years of cones that formed in prior years, but measurable decreases in survival-enhancing traits
405 such as resin ducts or growth of xylem with high hydraulic safety.

406 A switch to a flight response need not require mortality after reproduction or initiation of
407 reproductive structures—only a shift to greater relative investment in reproduction. The terminal
408 investment hypothesis, which argues that organisms may allocate resources preferentially to
409 reproduction immediately prior to death or senescence (Clutton-Brock 1984) may not apply
410 directly to long-lived perennial polycarpic trees. Koenig et al. (2017) present one of the first
411 direct assessments of terminal investment in polycarpic trees, and find little support for it in
412 Valley Oak (*Quercus lobata*). This conclusion is based on there being no tradeoff between
413 growth and reproduction, and no change in seed production at the stand scale prior to mortality.
414 However, this study did not examine tradeoffs between reproduction and growth in
415 geographically constrained populations undergoing a stress-induced mass mortality event.
416 Instead, only 0.7% of observed trees died “apparently of natural causes” across a large
417 geographic range, and the lack of observable tradeoffs may be a result of natural patterns of
418 senescence versus switches in resource allocation in terminally stressed trees. Thus terminal

419 investment may still apply in highly stressed tree populations, but evidence is limited. More
420 likely, trees that increase C allocation to reproduction under drought stress may be somewhat
421 reducing allocation to survival traits, but not to the point of ensuring their own death.

422 Differential rates of continued investment of resources into reproduction that was
423 initiated prior to stressful conditions can be categorized as fight or flight. If a tree invests
424 resources into cone initiation and then resource availability drops, then we would expect an
425 increase in cone abortion rates as trees switch resource allocation toward survival as part of a
426 fight strategy (Figure 5A). A lack of increased abortion would then be indicative of continued
427 resource allocation to reproductive output (Figure 5B). If coupled with a decrease in investment
428 in fight responses, this would indicate a relative shift toward flight. If cone initiation and
429 development are triggered by a drought at the expense of growth, survival probability, or both
430 (Figure 5C), this would be a flight strategy tipping toward terminal investment.

431

432 **Evolutionary Implications**

433 From an evolutionary perspective, the effect of either of these behaviors on fitness
434 depends on climatic and competitive conditions. If a tree species experiences rapid climate
435 change, it must “migrate” via seed dispersal into newly favorable areas or adapt to new
436 conditions. If a tree cannot migrate or adapt, the species may experience a decrease in population
437 size or range (Aitken et al. 2008). This may reduce the relative fitness benefit of fight responses
438 when climatic stresses increase, as sexual reproduction generates new genetic combinations on
439 which natural selection can act locally, while dispersal enables migration to less climatically
440 stressful areas (Figure 6).

441 Investment in seed production does not guarantee successful recruitment of new
442 individuals into a population, let alone a successful range expansion or shift (Case and Taper
443 2000, Aitken et al. 2008). Recent work has demonstrated that reproductive effort in *P. ponderosa*
444 is expected to increase under climate change, but that the same conditions that benefit
445 reproductive output may reduce seedling recruitment, leading to a net decrease in *P. ponderosa*
446 range (Petrie et al. 2017). Increased reproduction does, however, increase adaptive potential in
447 long-lived plants. Climent et al. (2008) show that early investment in reproduction may be an
448 ideal strategy for trees that have serotinous cones, as building an early aerial seedbank can
449 increase overall fitness in areas prone to stand-replacing fires. Reproductive investment at an
450 earlier age than most *Pinus* species has been observed in both *P. halepensis* and *P. pinaster*
451 (Climent et al. 2008, Santos-del-Blanco et al. 2012), which both live in fire-prone landscapes
452 with high-severity burns, demonstrating potential selection for high reproductive output in a
453 disturbance-prone landscape. Tree species can exhibit “adaptation lag,” whereby the rate of
454 genetic change is much slower than that of climate change (Aitken et al. 2008). Modeling studies
455 have shown that increased adult mortality could potentially reduce this adaptation lag by
456 allowing better-adapted seedling genotypes to regenerate more quickly in the resulting gaps
457 (Kuparinen et al. 2010). Further, increased allocation of C and N to seeds has been shown to
458 increase germination potential, demonstrating the simultaneous benefit of increased seed output
459 and potential recruitment in trees investing more resources in seed (Caliskan and Makineci
460 2015). Thus, flight strategies may increase adaptive potential in stressful environments.

461 One caveat of the framework presented here is the response of a tree to stress may be
462 affected by pre-stress growth patterns. Trees that grew vigorously when immature may be more
463 susceptible to stress when mature, because fast growing trees may be more likely to be attacked

464 by wood-boring insects and defoliators (Ruel and Whitham 2002). A tree can thus exhibit
465 drought avoidance strategies in the current year and still be at risk of drought stress due to prior
466 growth patterns. If a tree has already grown “safe” xylem (i.e. tracheids with high t/D), then
467 decreased overall growth may actually be the best strategy. Such a strategy may then allow a tree
468 to store more C in pools for later use. If a tree has inefficient or unsafe xylem, then rapid growth
469 of safe xylem or root tissue may be the most beneficial strategy, depending on current leaf area.
470 If leaf area is high, then high K must be maintained—potentially at the expense of hydraulic
471 safety—in order to maintain canopy hydration (Pittermann, personal communication).
472 Regardless, we hypothesize that as drought intensity or length increases, the fitness benefit of a
473 reproductive flush is increased.

474

475 **Implications for Future Research**

476 The tradeoffs discussed above (reproduction-growth and growth-hydraulic safety) are not
477 new concepts. Nor is the idea of tradeoffs between various survival-enhancing tree traits under
478 stress (Ferrenberg et al. 2015). However, no research to date has synthesized both sets of
479 tradeoffs into an integrative C budget model for trees under stress. The conceptual framework
480 presented here identifies multiple targets for future research. If conifer populations do exhibit
481 stress-induced flight behaviors, this would represent a significant shift in our understanding of
482 the implications of drought stress on tree populations. We hypothesize that the tradeoffs inherent
483 in wood growth in coniferous trees are exacerbated by drought in ways that can have
484 counterintuitive effects on cellular physiology and reproductive output. We propose that “flight”
485 strategies may increase fitness in stressful environments. To test this hypothesis, we must
486 examine models of C allocation with the context of extreme environmental gradients. Recent and

487 current studies continue to provide new insights into formation, concentration, and mobilization
488 of NSC storage pools (Oberhuber et al. 2011, Aaltonen et al. 2016, Guo, et al. 2016a, Birami et
489 al. 2018, Li et al. 2018), which will greatly increase understanding of conifer C storage
490 dynamics.

491 Seed production and seed quality are areas in need of continued research. Comprehensive
492 models of seed production that incorporate data from simple field methods (Clark et al. 1999,
493 Sánchez et al. 2011) should be employed in studies of C dynamics to scale from individual tree
494 physiology to patterns of seed production. Additional research is needed to quantify C
495 investment in cone and seed tissue, as well as what variation in investment to cones and seeds
496 means for germination success. Thus, future studies of forest drought response should
497 incorporate cone and seed collections or counts as well as adult tree physiology. The greatest
498 opportunity for integration of multi-scale measurements of tree responses to climate change is in
499 the joining of wood anatomy and tree ecology (Locosselli and Buckeridge 2017). Recent
500 advances in the fields of tracheid anatomy and phenology demonstrate the temporal information
501 that can be gathered from observing xylem production relative to climate stress in situ, including
502 timing of xylem formation, tracheid widening, and wall thickening (Rossi et al. 2012, Ziaco and
503 Biondi 2016). These kinds of observational studies can be paired with reproductive surveys, ¹³C
504 pulse-labeling experiments (Heinrich et al. 2015), and further chemical partitioning of wood (i.e.,
505 measurement of lignin concentrations) to understand the xylem-level tradeoffs that may occur
506 under stress. Modern instrumentation can also be leveraged to measure everything from growth
507 dynamics to sap flow and NSC concentrations all on a single tree in an automated fashion.
508 Steppe et al. (2015) outline an idealized study system utilizing instrument clusters to pair
509 ecophysiological and anatomical measurement, allowing a high-resolution, real-time tracking of

510 growth dynamics along with potential C allocation patterns. These kinds of studies could then be
511 used to further test for evidence of fight or flight behavior by incorporating simple reproductive
512 surveys. Finally, hierarchical modeling techniques can use the conceptual model presented here
513 as a foundation for building trait-based predictions of whole-forest or species-level range shifts
514 in response to climate change (Rehfeldt et al. 2015, Garcia-Forner et al. 2016, O'Brien et al.
515 2017).

516 Climate change-induced mortality in forests can be leveraged as a “natural experiment”
517 to evaluate differences between living and stress-killed trees (Gleason et al. 2017). The
518 widespread, drought-induced mortality of conifers in Western North America (Hicke et al. 2016,
519 Young et al. 2017) provides an ideal system for examining drivers of differential mortality and
520 survival at small scales. Such drivers may include variation in the cellular components of growth
521 (e.g., variation in xylem anatomy) relative to reproductive output, as well as the degree of
522 tradeoff between hydraulic architecture and seed production. As climate change continues to
523 apply novel stresses to tree populations, forest ecologists and tree physiologists must develop
524 methods to test not only current response to stress, but also how responses at multiple spatial
525 scales affect whole-forest response. Some species and individuals may fight, and invest all
526 available resources into survival at the risk of succumbing to long-term or permanent climatic
527 stress. Others may exhibit flight behavior, putting resources toward seed, which may increase
528 migration or adaptation potential. Our understanding of these responses can be enhanced by not
529 only developing conceptual and numeric models of C allocation within a tree, but also how that
530 allocation affects future C allocation, tradeoffs, and feedbacks among tree processes. Fine-scale
531 mechanistic studies of tree physiology continue to use novel approaches that should now be
532 combined into integrative models of tree response to changing climate.

533

534 Acknowledgments

535 This article was first developed in a Global Change Biology course taught by EVM and further
536 refined in Advanced Topics in Ecology, taught by SCH at UCM. We would like to acknowledge
537 the Southern Sierra Critical Zone Observatory (CZO), Sequoia National Park, and the USDA
538 Forest Service for facilitating fieldwork that supported conception of the hypotheses presented
539 here. We thank Melaine Aubry-Kientz, Mengjun Shu, and anonymous reviewers for helpful
540 comments on this manuscript.

541

542 Funding

543 This work was partially funded by fellowships (JDL) from Southern California Edison, and the
544 National Science Foundation through the Southern Sierra CZO (EAR-1331939) and CZO
545 Science Across Virtual Institutes (SAVI) program (ICER-1445246), and National Geographic
546 grant CP-062ER-17 (JDL).

547

548 Author Contributions

549 JDL developed initially the ideas and hypotheses in this synthesis, and led the writing of the
550 manuscript. EVM and SCH contributed conceptually to revisions, and all authors edited and
551 substantially revised manuscript drafts and provided final approval for publication.

552

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897 **Table 1.** Reported positive (+) or negative (-) relationships between growth and cone production
 898 or drought and cone production in studies directly assessing reproduction in conifer species.
 899 Spearman ρ and Pearson r correlation coefficients or estimated β values from original fitted
 900 models are reported where present or calculated from published data. Correlations between final
 901 cone production and climatic values in the inferred year of initiation, pollination, or maturation,
 902 if specified, are presented. Calculated values are shown in italic, and values shown are species
 903 averages if values were from multiple plots in a single location, or averaged across all
 904 reproductive stages (for Growth-Total R correlations). Total R = total cone production. Values in
 905 parentheses are S.D.;n for species averages across sites or reproductive stages.

Species	Growth: Total R	Drought: Initiation	Drought: Pollination	Drought: Maturation	Drought: Total R	Reference
<i>Abies sachinensis</i>	+					Hisamoto and Goto 2017
<i>Pinus banksiana</i>	+0.05 (0.02;3) _a	0.32 ^a	0.05 ^a	-0.16 ^a		Riemenschneider 1985, Despland and Houle 1997
<i>Picea engelmannii</i>	+				+	Buechling et al. 2016
<i>Pinus pinea</i>	+					Gonçalves and Pommerening 2012
<i>Pinus sylvestris</i>	0.355 ^b				-	Vilà-Cabrera et al. 2014
<i>Abies alba</i>	-	0.55 ^b	-0.53 ^b	-		Davi et al. 2016
<i>Abies lasiocarpa</i>	+/-	0.1(0.45; 12) ^c	0.05 (2.95;12) ^c	0.1(0.45; 12) ^c		Woodward and Silsbee 1994
<i>Tsuga mertensiana</i>	+/-	-0.075 (0.575;12) ^c	0.075 (0.375;12) ^c	-0.075 (0.575;12) ^c		Woodward and Silsbee 1994
<i>Pseudotsuga menziesii</i>	-				+	Ebell 1967, Eis et al. 1965
<i>Pinus edulis</i>		≤ -0.51 ^{c*}				Redmond et al. 2012
<i>Picea glauca</i>		-0.29 ^b	0.47 ^b	-0.25 ^b	+	Roland et al. 2014
<i>Pinus palustris</i>					+	Guo et al. 2016b
<i>Pinus pinea</i>		-0.01 ^b				Calama et al. 2011
<i>Pinus ponderosa</i>		≤ -0.35 ^c			-0.61 ^b	Mooney et al. 2011, Keyes and González 2015
<i>Pinus taeda</i>		+				Greenwood 1981
<i>Pinus halepensis</i>			-(female) +(male)	+(Spring) - (Summer)		Girard et al. 2012, Thabeet et al. 2009

^aSpearman's ρ , ^b β estimate for reproduction term in fitted model (see reference for model), ^cPearson's r

*Temperature stress only

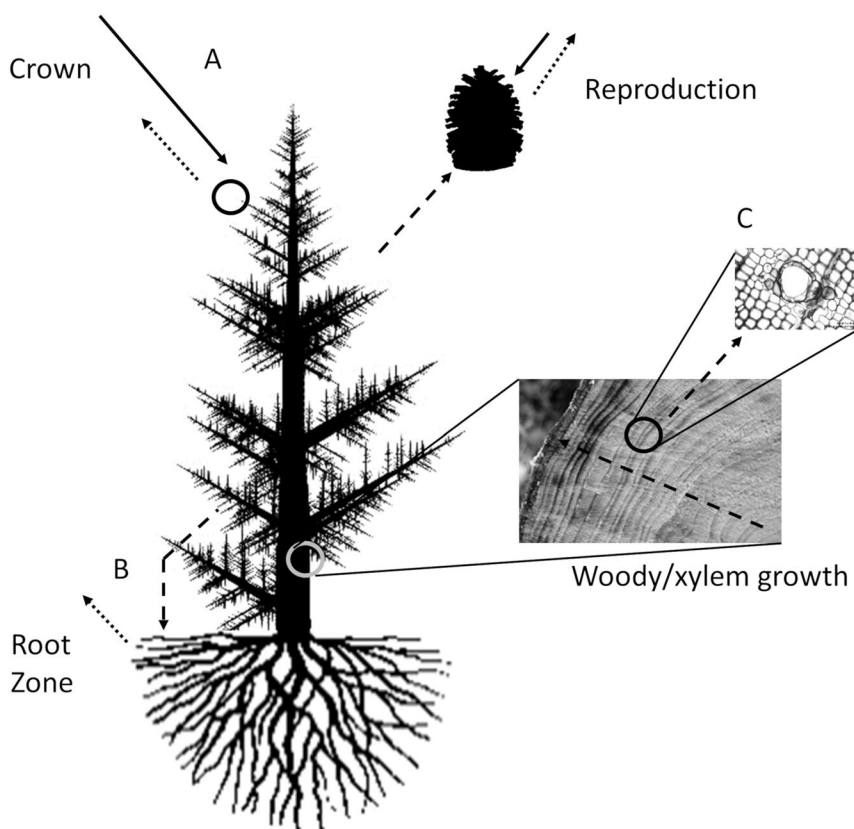
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909 **Figure Legends**

910 **Figure 1.** Conceptual diagram depicting potential tradeoffs in carbon (C) allocation in coniferous
 911 trees. Solid arrows represent C uptake (photosynthesis), dotted arrows represent C loss
 912 (respiration), and dashed arrows represent C allocation pathways. If C is allocated to seed
 913 production, that C is no longer available for leaf production (and associated photosynthesis, A),
 914 root production (B), or radial growth, which itself influences hydraulic conductivity and
 915 resistance to pests (as a function of tracheid size and resin duct formation, C).
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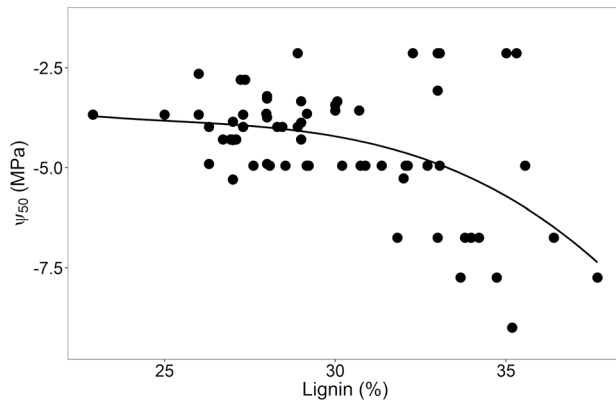
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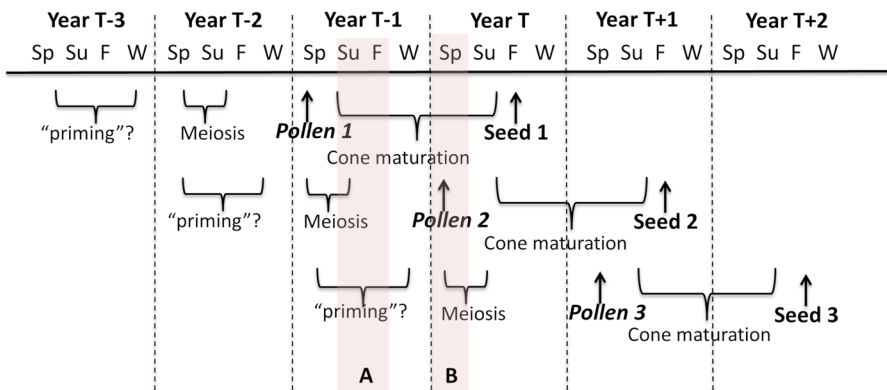
929 **Figure 2.** Relationship between total wood lignin concentration (%) and Ψ_{50} , the water potential
 930 at which 50% of conductivity is lost, in 25 gymnosperm species distributed globally. $R^2 = 0.20$,
 931 $P = 0.0007$. Data from (Pereira et al. 2018) and (Choat et al. 2012). Lignin data from multiple
 932 wood sources (branch or stem), and is assumed to scale linearly between sampled organs (see
 933 Pereira et al. 2018 for sample inclusion criteria).

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965 **Figure 3.** Potential effects of two given drought events (shaded boxes A and B) on reproductive
 966 output in masting conifers relative to a given year (T). Conifer cone production occurs over two
 967 to three years, and the effects of drought on resource availability for masting can have both direct
 968 effects (e.g., decreased reproduction in a year of drought) or indirect effects (e.g., increased
 969 reproduction in subsequent years due to increased C storage) depending on the reproductive
 970 stage. Arrows in figure represent timing of each reproductive stage. Arrows below figure
 971 represent relative change in each reproductive stage, with the expected mechanism of this change
 972 given in parentheses.
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A) Dry summer/fall year T-1:

Direct effects: ↓ Seed 1 (C limitation) ↓ Seed 3 (N limitation during priming)

Indirect effects: ↑ Seed 2 (increased C availability)

B) Dry spring year T:

Direct effects: ↓ Seed 1 (C limitation) ↓ Seed 3 (poor meiosis) ↑ Seed 2 (good pollination)

Indirect effects: ↑ Seed 2 (low Seed 1) ↓ Seed 3 (high Seed 2)

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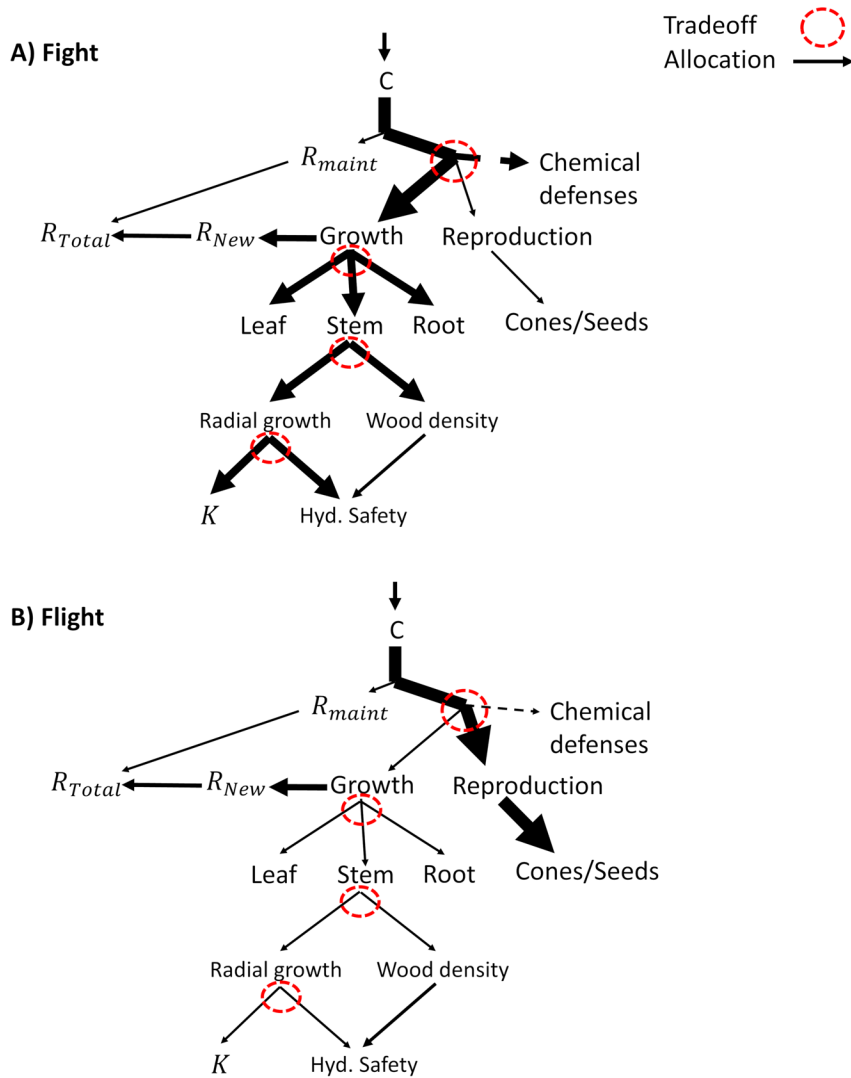
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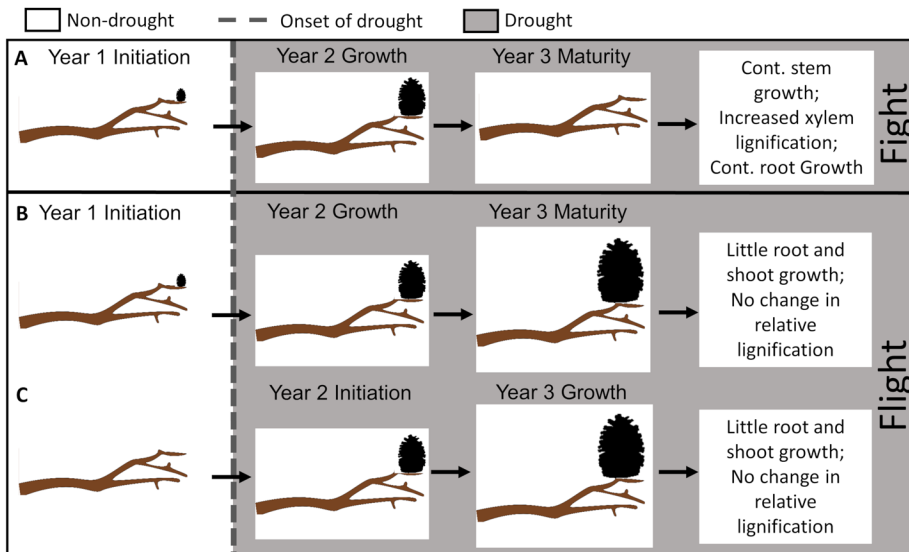
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990 **Figure 4.** Theoretical expectations of a “fight” response (A) or a “flight” response (B) in conifers
 991 under drought stress. Line weight represents the relative magnitude of carbon (C) allocation to
 992 that particular plant pool following a tradeoff induced by drought stress. Fight responses are
 993 demonstrated by allocation of available resources to growth or drought or pest defenses at the
 994 expense of reproductive allocation. Flight responses occur when a tree allocates C to cone and
 995 seed production at the expense of growth and drought defense or pest defense. C = carbon pool,
 996 R = respiration, Hyd. Safety = hydraulic safety, K = sapwood conductance.
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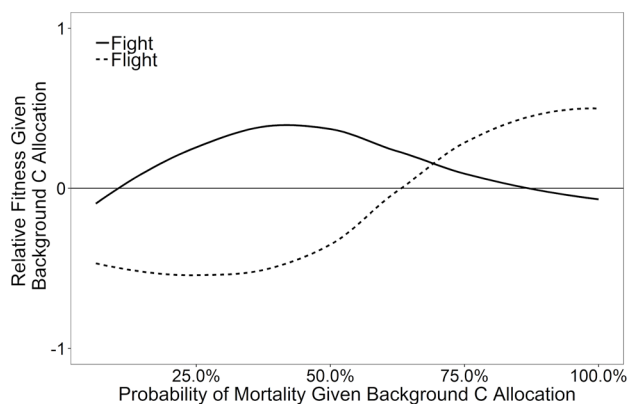
1004 **Figure 5.** Multiple strategies for “flight” behaviors relative to prior reproductive investment. If a
 1005 drought occurs after cone initiation, cone abortion and re-allocation of resources to growth and
 1006 drought defense is an indicator of “fight” behaviors (A). On the other hand, if cones are not
 1007 aborted but maintained through their maturation under drought stress, this can be considered a
 1008 flight behavior (B). The final observable flight behavior is drought-induced reproduction (C),
 1009 which may or may not be associated with terminal investment prior to mortality.
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1013 **Figure 6.** Hypothetical increase or decrease in fitness versus expected “background” fitness of
 1014 “fight” or “flight” behaviors relative to the likelihood of mortality under drought stress. As
 1015 likelihood of drought-induced mortality increases (e.g., with increased drought intensity and
 1016 duration), the relative benefit of fight behaviors may decrease as drought defenses fail and trees
 1017 die without reproducing. Flight behaviors provide little increased fitness benefit when the
 1018 probability of mortality is low, but provide significantly higher fitness increases as probability of
 1019 mortality increases. This is because flight behaviors increase potential future recruitment of new
 1020 seedlings and capacity for adaptation to a drier climate or migration to track a more optimal
 1021 climate.
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