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

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Abstract

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

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

Introduction

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

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

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

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

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

1998) decreases CO_2 uptake (Farquhar and Sharkey 1982) and availability of C for growth or reproduction (McDowell et al. 2008). Recent work has attempted to parse mechanisms of drought-induced mortality from both a physiological and C availability perspective (McDowell et al. 2008, McDowell 2011, Kerhoulas and Kane 2012, Anderegg et al. 2012, Sala et al. 2012, Anderegg and Anderegg 2013, Sevanto and Dickman 2015, Adams et al. 2017, Birami et al. 2018). However, there has been little synthesis across studies of drought-response physiology and life history tradeoffs, and several prominent unanswered questions remain. These include: How do climate and individual life history traits influence stress avoidance strategies?; Is there an optimal strategy of resource use that allows for both survival and the highest chance of successful reproduction under stressful conditions?; and what are the implications of tradeoffs between survival and reproduction for species persistence under climate change? Answering these questions requires a more robust scaling of mechanistic drought responses from the individual cell to the whole tree with respect to both survival and reproduction.

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

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

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

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

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

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

Tracheid walls are mostly composed of cellulose and hemicellulose (primary cell wall) and lignin (secondary wall). In conifers, radial growth is often positively correlated with tracheid abundance and size, with larger ring widths being associated with more numerous and thinner-walled tracheids (Xu et al. 2014, Cuny et al. 2014). Tracheid wall thickness is positively correlated with lignin concentrations (Gindl 2001). Lignin contains, on average, 30% more energy (in the form of C) than cellulose (White 2007, Novaes et al. 2010). High negative correlations have been shown between total tree biomass and lignin concentrations (Novaes et al. 2010), demonstrating that decreased radial growth is often associated with increased relative lignin (and thus increased C cost) per unit volume of wood. Lignin concentration in gymnosperms is negatively correlated with Ψ50 (the water potential at which 50% of conductivity is lost, Figure 2). This is likely due to tracheid wall reinforcement, but there is also mixed evidence of lignin deposition into the various components of inter-tracheid pit membranes that may alter embolism resistance (Pereira et al. 2018). While the role of lignin in reducing likelihood of cavitation must be further explored, this data demonstrates that constructing drought-resistant xylem is lignin intensive. Thus, the tradeoffs among radial growth, xylem hydraulic safety, hydraulic efficiency, and the C cost of all three of these components show that growth and "type" of growth (i.e., high or low radial growth versus hydraulic safety) are only loosely dependent, and may be independent under drought stress. For example, two trees may grow rings of equal width, but with significantly different hydraulic safety and relative C investment; radial growth and hydraulic safety do not necessarily constrain each other, but may if resources are depleted.

The C costs of growth-related structures are further exacerbated by the multiple interactive stresses often placed on trees during drought. In many coniferous forests, for example, outbreaks of wood-boring insects and other pests coincide with drought stress due to weakened pest defenses and ideal conditions for pest proliferation (Hicke et al. 2016). Both chemical and physical defenses to pests represent a significant C cost (Franceschi et al. 2005). The quantity of resin ducts, which transport C-based defensive compounds, and the ratio of resin ducts to xylem cells, are both positively correlated with survival of bark beetle attack in conifers (Kane and Kolb 2010, Ferrenberg et al. 2014). Tree growth and resin duct properties (including duct density) are also positively correlated, suggesting that conditions conducive to growth are also conducive to increased defenses (Kane and Kolb 2010, Ferrenberg et al. 2014), likely due to high availability of resources, including C. While resin duct formation tends to decrease under drought stress (Slack et al. 2017), allocation of resources to resin ducts can rise when trees are deprived of phosphorus (Ferrenberg et al. 2015), showing that different stresses can induce different changes in resource allocation to pest defense. Thus a tradeoff exists between stress defense (both drought and pest) and other resource sink demands, such as growth or reproduction.

Mast seeding and carbon costs

Average construction costs of seed vary and are not always significantly different from leaf and stem tissue, but maximum seed construction costs are often much higher than other tissues (Poorter et al. 2006). Reproductive structures can consume 6-10% of annual net canopy photosynthesis (Gower et al. 1995). Immature conifer cones can photosynthesize, but McDowell et al. (2000) reported that cone photosynthesis in *Pseudotsuga menziesii* can only provide about 27% of the C cost of cone production. The remaining C for cone formation must come from current photosynthetic activity or via drawing on C stores. Some data suggest potential C-limitation of reproduction. For instance, CO_2 fertilization of *P. taeda* induces larger cones and earlier seed production relative to tree size than under ambient conditions (Way et al. 2010).

Similarly, *P. taeda* trees exposed to elevated CO_2 produced three times as many cones and were twice as likely to be reproductively mature as trees of the same size grown in ambient conditions (LaDeau and Clark 2001).

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

Weather may affect particular stages of reproduction in different ways (Figure 3, Table 1). For instance, in species where the source of C for reproduction has been studied, spring reproductive structures (flower or immature female/pollen cones) tend to be built with stored C, while most of the C for developing fruits or cones comes from current-year assimilation (Hoch et al. 2003). Thus, weather conditions favorable for photosynthesis (relatively moist, moderately warm) during the seed development period are likely to be associated with larger seed crops (Keyes and González 2015, Guo et al. 2016b). However, the amount, synchrony, and effectiveness of pollen dispersal, which sets the stage for fruit/cone development, is often favored by dry, warm, or dry and warm spring conditions (Koenig et al. 2015, Pearse et al. 2016, Bogdziewicz et al. 2017, Gallego Zamorano et al. 2018). The pollen dispersal stage in turn depends on the development of flower/cone primordia and the meiosis that produces the precursors of ovules and pollen. This is often favored by warm conditions in the previous spring and summer (Smaill et al. 2011, Bogdziewicz et al. 2017, Gallego Zamorano et al. 2018), though that is not universal (Mooney et al. 2011), and may depend on whether the species is more limited by cold or drought. Finally, in at least some species, the year prior to primordia formation seems to be important for "resource priming" (Buechling et al. 2016), and the uptake of nitrogen (N) and other nutrients incorporated at this stage is often favored by moist, cool, or moist and cool conditions (Mooney et al. 2011, Smaill et al. 2011).

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

There is mixed evidence for tradeoffs among growth and reproduction during drought (Table 1). Tree growth is often decreased both during mast years and one year following masts (Hacket-Pain et al. 2017, Hacket-Pain et al. 2018). While positive correlations between growth and reproduction in non-masting years have been observed in *Pinus halepensis* (Santos et al. 2010, Ayari et al. 2012, Ayari and Khouja 2014), *P. pinaster* (Santos et al. 2010), *P. banksiana* (Despland and Houle 1997), and *Abies sachinelensis* (Hisamoto and Goto 2017), none of these studies explicitly assessed the growth-reproduction relationship in mast years versus non-mast years. Woodward and Silsbee (1994) found that both *A. lasiocarpa* and *Tsuga mertensiana* showed positive correlations between growth and reproduction overall, but that large cone crops (i.e., mast years) were associated with decreased radial growth. Koenig and Knops (1998) found negative correlations between vegetative growth and reproductive output over multiple years in both *Picea* and *Pinus* spp., and argue that this is direct evidence of a “switch” in C allocation between mast events. Eis et al. (1965) found that ring widths in *P. menziesii* over a 28-year period were only depressed during years of large cone crop production. Finally, a recent experimental study found that pines from which developing cones were removed grew marginally more immediately after the treatment, and also produced 70% more cones the year after, compared to control trees (Santos-del-Blanco et al. 2012). This suggests that resources may be mostly or entirely allocated to reproduction but re-allocated following cone removal.

Drought impacts on reproduction

Reproductive response of conifers to drought stress varies widely (Table 1). Direct evidence of drought-induced reproduction in conifers is mixed, and often difficult to directly assess (Davi et al. 2016). In part, this may be because, as mentioned above, climatic conditions can influence reproductive allocation during cone initiation, growth, and maturation differently. Consistent with the favorable impacts of dry conditions on pollination, several studies in conifers have found either negative correlations between initial male and female cone production and precipitation (Roland et al. 2014), or positive associations between water stress and initial female cone production (Greenwood 1981, Riemenschneider 1985). On the other hand, wet years are better for C assimilation, and have been found to be positively associated with the initiation of cone primordia (Mooney et al. 2011) or the development of fertilized cones (Roland et al. 2014, Keyes and González 2015, Guo et al. 2016b).

Because cone production is usually a multi-year process, a switch in C allocation toward greater relative investment in growth than reproduction during a low-resource year would likely result in abortion of currently developing cones. Cone abortion in conifers does appear to be higher in subdominant trees than dominant trees under ambient conditions (Goubitz et al. 2002). This may be the result of decreased CO_2 under light limitation (Berdanier and Clark 2016), leading to abortion of cones whose development cannot be safely supported. Thus, one potential direct indicator of altering C allocation to reproduction or growth under drought stress would be drought-induced increases in cone abortion rates, as trees shunt resources from cone production back into growth, drought defense, or pest defense.

Fight or Flight

Tradeoffs between growth, defenses, and reproduction

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

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

No current conceptual models of C allocation partition growth apportionment into sub-categories, such as hydraulic architecture versus radial growth. While radial growth produces new xylem, the anatomy of the xylem that makes up that radial growth can vary widely from year-to-year or tree-to-tree, affecting hydraulic safety. Few models of C allocation distinguish "types" of radial growth, such as the C cost of high radial growth with low wood density (and associated low hydraulic safety) versus the cost of low radial growth with high wood density. Such partitioning is important to fully understand the fitness implications of C allocation. Low stem radial growth is often predictive of mortality (Das et al. 2007), but lack of growth cannot be deemed drought intolerance if the tree is re-partitioning available resources to other "fight" behaviors that increase survival probabilities (e.g., decreased growth as a function of increased tracheid lignification, increased defensive chemicals, or increased root growth). Tradeoffs may occur not only between reproduction and growth, but also between growth of different tissues (i.e., stem, leaf, or root), and between different components of tissue growth, such as tracheid widening versus thickening.

Physiological mechanisms of tradeoffs

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

Under drought, high *K* does not always increase survival. In fact, high *K* relative to hydraulic safety (i.e., low xylem wall thickness or inter-tracheid pit resistance to cavitation) may increase risk of mortality (Pittermann et al. 2006b). Drought stress will likely lead to increased investment in wall thickening in newly grown tracheids, and to decreases in *K*. Turgor-limited cell expansion provides a mechanism for this shift. Cellular radial growth is constrained by the amount of water present, which drives tracheid cell enlargement prior to wall lignification and cell death (Woodruff et al. 2004). Cell lumen diameter is highly dependent on how long turgor can be maintained; the longer the expansion phase, the larger the lumen diameters and the smaller the t/D of the cell (Anfodillo et al. 2012). If a plant is drought stressed, cell turgor tends to be reduced, leading to drought-induced decreases in new xylem cell diameters and a relative increase in wall thickness (Cuny et al. 2014). This would result in a decrease in *K*, which may signal defoliation and thus reduced photosynthetic capacity. Further, a decrease in *K* via decreased tracheid lumen diameters and increased wall thickness would result in an increase in the relative C cost per unit volume of wood produced. Thus, the relationship between *K*, photosynthetic capacity, and hydraulic safety represents a positive feedback loop; drought would induce smaller tracheids with a higher hydraulic safety and higher relative C cost, which is further exacerbated by decreased C uptake potential.

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

Conceptual model of C allocation tradeoffs

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

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

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

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

A switch to a flight response need not require mortality after reproduction or initiation of reproductive structures—only a shift to greater relative investment in reproduction. The terminal investment hypothesis, which argues that organisms may allocate resources preferentially to reproduction immediately prior to death or senescence (Clutton-Brock 1984) may not apply directly to long-lived perennial polycarpic trees. Koenig et al. (2017) present one of the first direct assessments of terminal investment in polycarpic trees, and find little support for it in Valley Oak (*Quercus lobata*). This conclusion is based on there being no tradeoff between growth and reproduction, and no change in seed production at the stand scale prior to mortality. However, this study did not examine tradeoffs between reproduction and growth in geographically constrained populations undergoing a stress-induced mass mortality event. Instead, only 0.7% of observed trees died "apparently of natural causes" across a large geographic range, and the lack of observable tradeoffs may be a result of natural patterns of senescence versus switches in resource allocation in terminally stressed trees. Thus terminal investment may still apply in highly stressed tree populations, but evidence is limited. More likely, trees that increase C allocation to reproduction under drought stress may be somewhat reducing allocation to survival traits, but not to the point of ensuring their own death.

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

Evolutionary Implications

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

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

One caveat of the framework presented here is the response of a tree to stress may be affected by pre-stress growth patterns. Trees that grew vigorously when immature may be more susceptible to stress when mature, because fast growing trees may be more likely to be attacked by wood-boring insects and defoliators (Ruel and Whitham 2002). A tree can thus exhibit drought avoidance strategies in the current year and still be at risk of drought stress due to prior growth patterns. If a tree has already grown "safe" xylem (i.e. tracheids with high t/D), then decreased overall growth may actually be the best strategy. Such a strategy may then allow a tree to store more C in pools for later use. If a tree has inefficient or unsafe xylem, then rapid growth of safe xylem or root tissue may be the most beneficial strategy, depending on current leaf area. If leaf area is high, then high K must be maintained—potentially at the expense of hydraulic safety—in order to maintain canopy hydration (Pittermann, personal communication). Regardless, we hypothesize that as drought intensity or length increases, the fitness benefit of a reproductive flush is increased.

Implications for Future Research

The tradeoffs discussed above (reproduction-growth and growth-hydraulic safety) are not new concepts. Nor is the idea of tradeoffs between various survival-enhancing tree traits under stress (Ferrenberg et al. 2015). However, no research to date has synthesized both sets of tradeoffs into an integrative C budget model for trees under stress. The conceptual framework presented here identifies multiple targets for future research. If conifer populations do exhibit stress-induced flight behaviors, this would represent a significant shift in our understanding of the implications of drought stress on tree populations. We hypothesize that the tradeoffs inherent in wood growth in coniferous trees are exacerbated by drought in ways that can have counterintuitive effects on cellular physiology and reproductive output. We propose that "flight" strategies may increase fitness in stressful environments. To test this hypothesis, we must examine models of C allocation with the context of extreme environmental gradients. Recent and current studies continue to provide new insights into formation, concentration, and mobilization of NSC storage pools (Oberhuber et al. 2011, Aaltonen et al. 2016, Guo, et al. 2016a, Birami et al. 2018, Li et al. 2018), which will greatly increase understanding of conifer C storage dynamics.

Seed production and seed quality are areas in need of continued research. Comprehensive models of seed production that incorporate data from simple field methods (Clark et al. 1999, Sánchez et al. 2011) should be employed in studies of C dynamics to scale from individual tree physiology to patterns of seed production. Additional research is needed to quantify C investment in cone and seed tissue, as well as what variation in investment to cones and seeds means for germination success. Thus, future studies of forest drought response should incorporate cone and seed collections or counts as well as adult tree physiology. The greatest opportunity for integration of multi-scale measurements of tree responses to climate change is in the joining of wood anatomy and tree ecology (Locosselli and Buckeridge 2017). Recent advances in the fields of tracheid anatomy and phenology demonstrate the temporal information that can be gathered from observing xylem production relative to climate stress in situ, including timing of xylem formation, tracheid widening, and wall thickening (Rossi et al. 2012, Ziaco and Biondi 2016). These kinds of observational studies can be paired with reproductive surveys, ^{13}C pulse-labeling experiments (Heinrich et al. 2015), and further chemical partitioning of wood (i.e., measurement of lignin concentrations) to understand the xylem-level tradeoffs that may occur under stress. Modern instrumentation can also be leveraged to measure everything from growth dynamics to sap flow and NSC concentrations all on a single tree in an automated fashion. Steppe et al. (2015) outline an idealized study system utilizing instrument clusters to pair ecophysiological and anatomical measurement, allowing a high-resolution, real-time tracking of growth dynamics along with potential C allocation patterns. These kinds of studies could then be used to further test for evidence of fight or flight behavior by incorporating simple reproductive surveys. Finally, hierarchical modeling techniques can use the conceptual model presented here as a foundation for building trait-based predictions of whole-forest or species-level range shifts in response to climate change (Rehfeldt et al. 2015, Garcia-Forner et al. 2016, O'Brien et al. 2017).

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

Acknowledgments

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

Funding

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

Author Contributions

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

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Table 1. Reported positive (+) or negative (-) relationships between growth and cone production or drought and cone production in studies directly assessing reproduction in conifer species. Spearman ρ and Pearson r correlation coefficients or estimated *β* values from original fitted models are reported where present or calculated from published data. Correlations between final cone production and climatic values in the inferred year of initiation, pollination, or maturation, if specified, are presented. Calculated values are shown in italic, and values shown are species averages if values were from multiple plots in a single location, or averaged across all reproductive stages (for Growth-Total R correlations). Total R = total cone production. Values in 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
Abies sachinelensis	+					Hisamoto and Goto 2017
Pinus banksiana	*+0.05 (0.02;3)*^{a}	0.32^{a}	0.05^{a}	-0.16^{a}		Riemenschneider 1985, Despland and Houle 1997
Picea engelmannii	+				+	Buechling et al. 2016
Pinus pinea	+					Gonçalves and Pommerening 2012
Pinus sylvestris	0.355^{b}				-	Vilà-Cabrera et al. 2014
Abies alba	-	0.55^{b}	-0.53^{b}	-		Davi et al. 2016
Abies lasiocarpa	+/-	*-0.1(0.45;12)*^{c}	*0.05 (2.95;12)*^{c}	*-0.1(0.45;12)*^{c}		Woodward and Silsbee 1994
Tsuga mertensiana	+/-	*-0.075 (0.575;12)*^{c}	*0.075 (0.375;12)*^{c}	*-0.075 (0.575;12)*^{c}		Woodward and Silsbee 1994
Pseudotsuga menziesii	-				+	Ebell 1967, Eis et al. 1965
Pinus edulis		$\leq -0.51^{c*}$				Redmond et al. 2012
Picea glauca		-0.29^{b}	0.47^{b}	-0.25^{b}	+	Roland et al. 2014
Pinus palustris					+	Guo et al. 2016b
Pinus pinea		-0.01^{b}				Calama et al. 2011
Pinus ponderosa		$\leq -0.35^{c}$			-0.61^{b}	Mooney et al. 2011, Keyes and González 2015
Pinus taeda		+				Greenwood 1981
Pinus halepensis			-(female) +(male)	+(Spring) -(Summer)		Girard et al. 2012, Thabeet et al. 2009

[a]Spearman's ρ, [b]*β* estimate for reproduction term in fitted model (see reference for model), [c]Pearson's r
[*]Temperature stress only

Figure Legends

Figure 1. Conceptual diagram depicting potential tradeoffs in carbon (C) allocation in coniferous trees. Solid arrows represent C uptake (photosynthesis), dotted arrows represent C loss (respiration), and dashed arrows represent C allocation pathways. If C is allocated to seed production, that C is no longer available for leaf production (and associated photosynthesis, A), root production (B), or radial growth, which itself influences hydraulic conductivity and resistance to pests (as a function of tracheid size and resin duct formation, C).

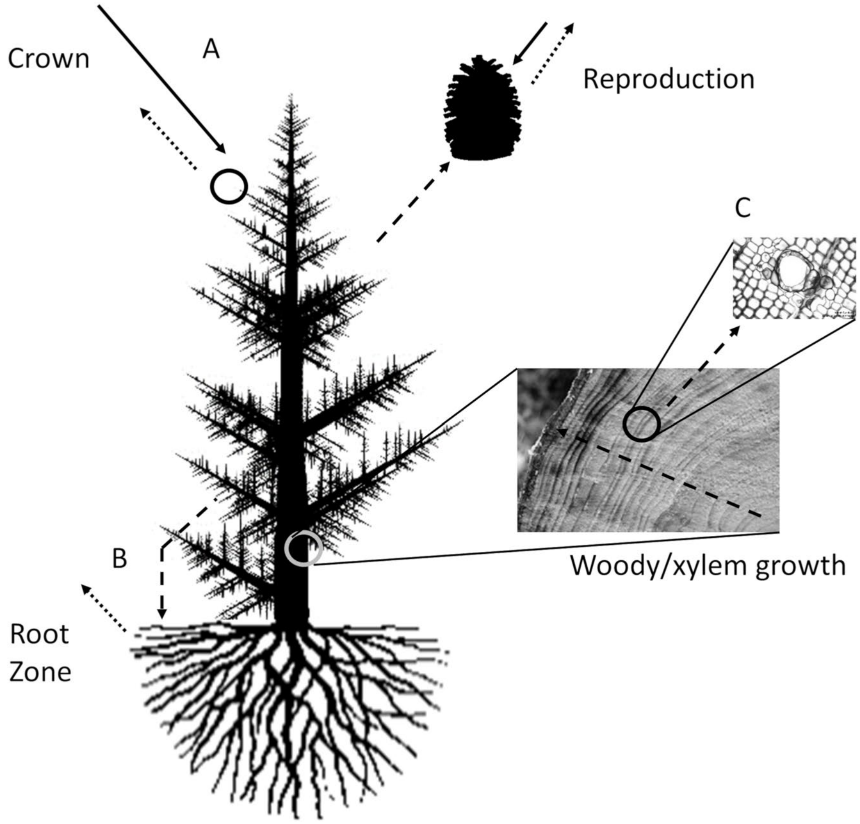


Figure 2. Relationship between total wood lignin concentration (%) and Ψ_{50}, the water potential at which 50% of conductivity is lost, in 25 gymnosperm species distributed globally. $R^2 = 0.20$, $P = 0.0007$. Data from (Pereira et al. 2018) and (Choat et al. 2012). Lignin data from multiple wood sources (branch or stem), and is assumed to scale linearly between sampled organs (see Pereira et al. 2018 for sample inclusion criteria).

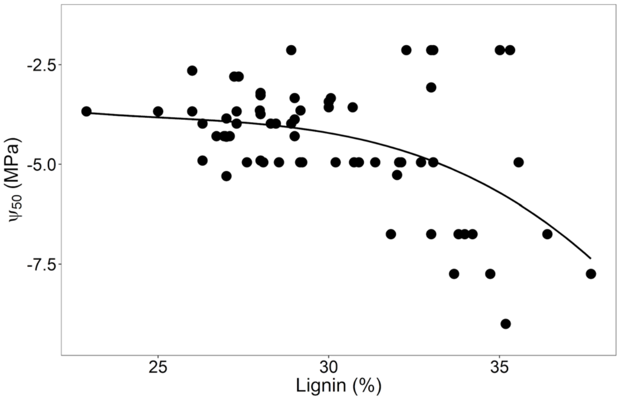
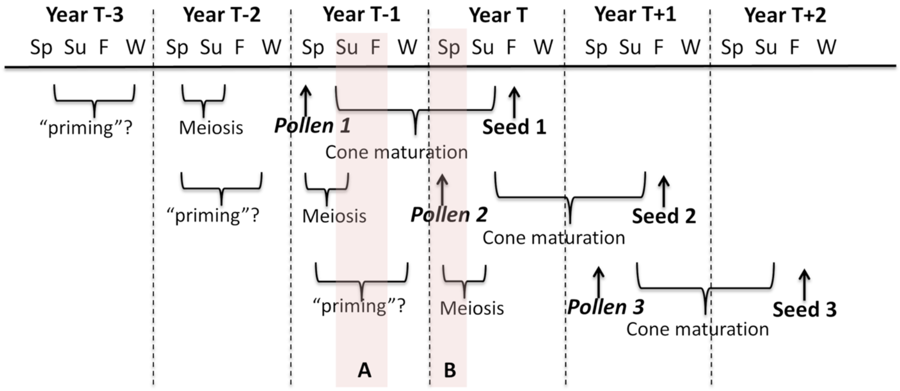


Figure 3. Potential effects of two given drought events (shaded boxes A and B) on reproductive output in masting conifers relative to a given year (T). Conifer cone production occurs over two to three years, and the effects of drought on resource availability for masting can have both direct effects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



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)

Figure 4. Theoretical expectations of a "fight" response (A) or a "flight" response (B) in conifers under drought stress. Line weight represents the relative magnitude of carbon (C) allocation to that particular plant pool following a tradeoff induced by drought stress. Fight responses are demonstrated by allocation of available resources to growth or drought or pest defenses at the expense of reproductive allocation. Flight responses occur when a tree allocates C to cone and seed production at the expense of growth and drought defense or pest defense. C = carbon pool, R = respiration, Hyd. Safety = hydraulic safety, *K* = sapwood conductance.

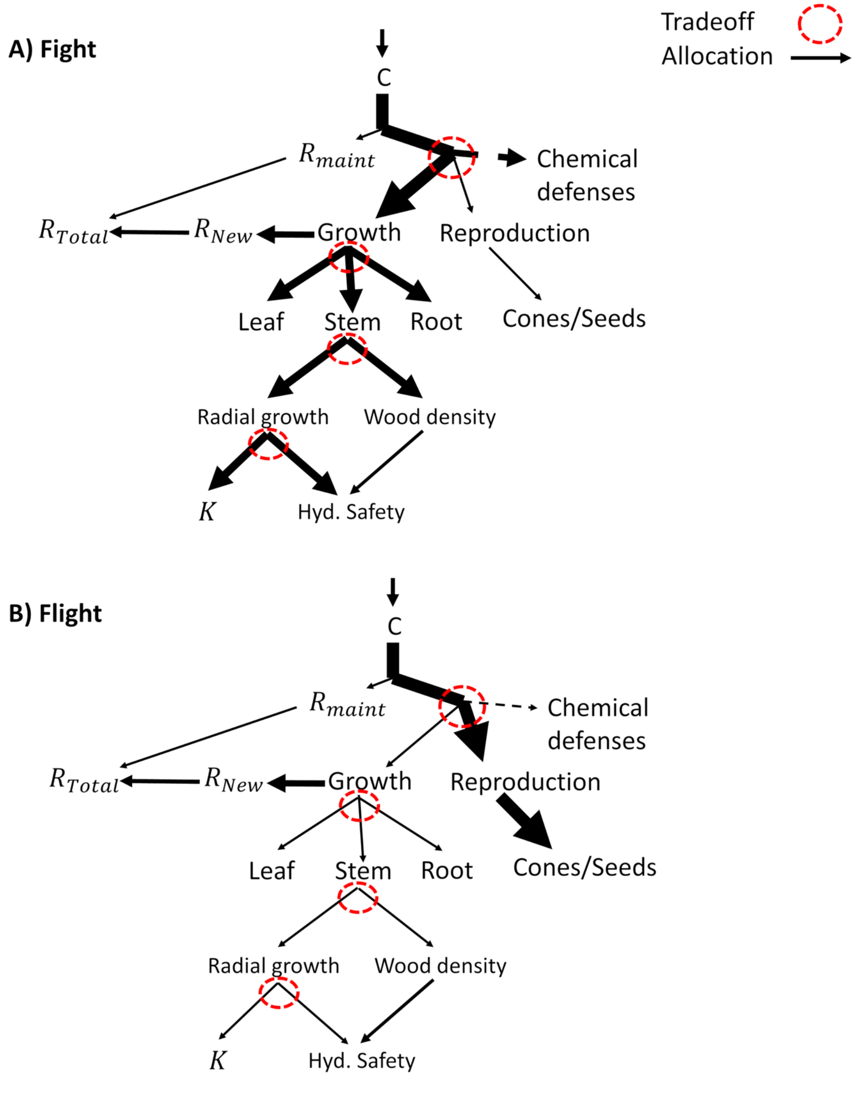


Figure 5. Multiple strategies for "flight" behaviors relative to prior reproductive investment. If a drought occurs after cone initiation, cone abortion and re-allocation of resources to growth and drought defense is an indicator of "fight" behaviors (A). On the other hand, if cones are not aborted but maintained through their maturation under drought stress, this can be considered a flight behavior (B). The final observable flight behavior is drought-induced reproduction (C), which may or may not be associated with terminal investment prior to mortality.

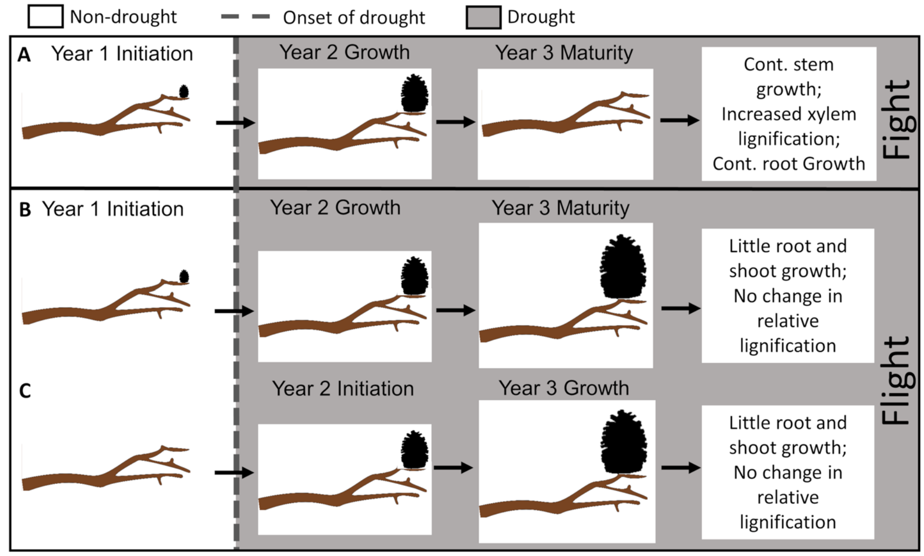


Figure 6. Hypothetical increase or decrease in fitness versus expected "background" fitness of "fight" or "flight" behaviors relative to the likelihood of mortality under drought stress. As likelihood of drought-induced mortality increases (e.g., with increased drought intensity and duration), the relative benefit of fight behaviors may decrease as drought defenses fail and trees die without reproducing. Flight behaviors provide little increased fitness benefit when the probability of mortality is low, but provide significantly higher fitness increases as probability of mortality increases. This is because flight behaviors increase potential future recruitment of new seedlings and capacity for adaptation to a drier climate or migration to track a more optimal climate.