nature ecology & evolution

SUPPLEMENTARY INFORMATION

DOI: 10.1038/s41559-017-0248-x

In the format provided by the authors and unedited.

A multi-species synthesis of physiological mechanisms in drought-induced tree mortality

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Supplementary Methods

PLC estimation from indirect measures. Plant xylem water potential was used to estimate PLC in four cases from studies 4, 12, 13, and 17 using hydraulic vulnerability curve (HVC) data from recent studies (see Supplementary Table 1 for specific studies). For these four cases, all HVCs were generated with the air injection method by the same researcher (PJ Hudson), from branches cut underwater and rehydrated for 24 hours under refrigeration (Wheeler et al. 2013), and data were fit with a Weibull curve. Data used to estimate PLC in *Eucalyptus globulus* branches were from 1-year old seedlings grown in 30 L pots in a glasshouse, sourced from an Australian nursery (Zeppel et al. unpublished data), analogous to the *E. globulus* used in study 4 (Mitchell et al. 2013, 2014). For *Pinus edulis* PLC estimation, we used two HVCs from mature trees of varying size growing in the field at two sites in New Mexico, USA, near Los Alamos (Garcia-Forner et al. 2016a) and at the Sevilleta experiment (study 14; Hudson et al., unpublished data). The Los Alamos HVC was used to estimate PLC for the mature, field-grown, *P. edulis* trees in study 17 because this curve was generated from trees located several miles from the mortality study. A mean of PLC estimates from both HVCs was used for the transplanted, small mature *P. edulis* from studies 12 and 13, which were sourced in New Mexico. Hydraulic conductance was used to model PLC in *P. edulis* from study 14 following the method of Sperry et al. (1998; Supplementary Table 1).

Additional wood density data sources. Wood density data were obtained for *Eucalyptus smithii* (Gardner 2001), *Juniperus osteosperma* (Chojnacky and Moisen 1993), *Nothofagus*

nitida (INN 2006), and directly from measurements of the experimental population of *Pinus edulis* in study 14.

Hydraulic trait data. Hydraulic trait data for the cases in which PLC was estimated using HVCs (Figure 1A) were from the same curves used in each case. To improve trait specificity to study populations, hydraulic safety margins were recalculated with minimum Ψ from the same population used in the mortality study, when possible, using the water potential value for stomatal closure.

Statistical analyses. To facilitate visual comparison of time series trends in NSCs from pre-drought to mortality, we found the best fit among linear, polynomial, logarithmic, power, and inverse regression models using Aikake's information criterion (AIC) for each case, where such data were available. NSC trend analysis was performed separately by tissue and fraction (total NSC, sugar, and starch). Time was normalized in these analyses to the maximum period of survival (i.e. time-to-mortality) before mortality and NSC components were normalized to maximum value in tissue NSCs. When differences among model fits were <5 points different in AIC, the simpler model was used. Care was taken not to over-fit polynomial models to trends when time points were limited. Non-significant time series trends were represented with a flat line at the mean normalized value. Differences in model fits among cases were not analyzed further.

Supplementary Discussion

Quantification of NSC changes. When NSCs at mortality were quantified as the change in NSCs from initial pre-drought to time of mortality (Supplementary Figure 6), the degree and direction of change were not always in agreement with NSC deviation from control, especially in angiosperms (Figure 1B, C, D; Supplementary Table 7). Examples include the large increase in percent change of NSCs in *Populus balsamifera* from pre-treatment to mortality, despite a reduction in NSCs relative to controls (Supplementary Table 7). This response may be the result of seedling exposure to cold temperatures later in this experiment, which generated accumulation of NSCs to facilitate osmotic cold tolerance (Galvez et al. 2013). Gymnosperm percent change in NSCs from initial pre-drought measurements to mortality was typically consistent with NSC differences between at mortality values and controls (Supplementary Table 7). In our conclusions, we primarily drew inferences from NSC data normalized relative to control values. Considering only the change in NSCs in dying trees without assessing NSC responses in surviving or control treatment trees is an imperfect metric for evaluating reduction in NSCs as it relates to carbon starvation. Carbon starvation via reserve exhaustion requires reduction of NSCs below critical (and currently unknown) survival thresholds that are likely to change seasonally with tree phenology and vary depending on environmental conditions, ontogeny, intra-species variability in tree structure and functional traits, and tree interaction with other organisms (e.g. pests, pathogens, grazers, mutualists). Therefore, comparison of dying trees to only pre-drought conditions, without concurrently measuring surviving or control trees, is likely ineffective in assessing carbon starvation. Moreover, a conclusive picture of the imbalance between C supply and demand may only be achieved when data on changes in NSC

68 concentrations are supplemented by data on changes in major supply and demand functions, such
69 as whole-plant assimilation, respiration and growth (Hartmann 2015).
70
71 **Limitations and research opportunities.** Specific thresholds that define the boundary for
72 survival or mortality during drought in PLC, and especially NSCs, are not well-resolved in the
73 literature, which represents a challenge for demonstrating the causality of mortality mechanisms.
74 Survival thresholds for PLC may depend on NSC availability for metabolic and osmotic function
75 that may be critical in resisting or even refilling xylem embolism under tension (Secchi and
76 Zwieniecki 2011). Several studies have used manipulation of light and CO_2 concentrations to
77 investigate the interdependence of hydraulic function and NSC reduction. Hartmann et al.
78 (2013a) found that *Picea abies* saplings exposed to drought died faster than those exposed to a
79 low CO_2 environment (20 to 75 ppm). Notably, saplings exposed to low CO_2 exhibited
80 significant NSC reduction in all tissues, while drought-exposed saplings showed NSC reductions
81 in roots only, indicating that drought-exposed saplings could not mobilize and use stored NSCs.
82 Quirk et al. (2013) exposed *Sequoia sempervirens* saplings to drought and 1500, 500, and 200
83 ppm CO_2. Their drought treatment was only lethal in the 200 ppm treatment, where saplings had
84 a significant decline in NSCs, which was not observed at higher CO_2 concentrations in non-lethal
85 treatments. O'Brien et al. (2014) manipulated NSCs in seedlings of ten tropical species prior to
86 drought by varying light intensity. During drought, low-NSC seedlings in all ten species died
87 earlier than high-NSC seedlings, although no decline in NSCs was observed in any tissue for all
88 ten species, and some low-NSC seedlings showed an NSC increase during drought. Sevanto et
89 al. (2014) found that *Pinus edulis* saplings under lethal drought and shade treatments had

reduced NSCs at mortality, but that the reduction in NSCs with shading was nearly double that of the drought treatment.

For carbon starvation, limited understanding of carbon metabolism, transport, and storage variability among organs, and over seasonal and annual timescales, inhibits our ability to determine the levels of reduced carbohydrates that are damaging or lethal (Hartmann 2015; Hartmann and Trumbore 2016). Moreover, many tree species store not only carbohydrates, but also substantial amounts of lipids, yet their role during drought has rarely been addressed (Fischer et al. 2015). Given the demonstrated interdependency between carbon starvation and hydraulic failure, future tree mortality studies should include multi-factor manipulation (e.g. temperature, nutrient availability, light, CO_2 concentration, biotic attack) needed to disentangle interacting processes in a time-series (see Duan et al. 2014, 2015). Few experiments have included multiple drought treatments that vary in intensity, although this affects tree hydraulics and carbon dynamics (Hartmann et al. 2013a), such that the characteristics of a mortality-inducing drought (e.g. duration and severity) may influence mortality mechanisms (McDowell et al. 2008). Since many widespread tree mortality events in recent decades have been associated with pest and pathogen attack, more research on the effects of biotic attack on drought-induced mortality processes are particularly needed (Allen et al. 2010; Oliva et al. 2014; Anderegg et al. 2015; Wiley et al. 2015).

Specific design recommendations for future studies. Our synthesis provides an opportunity to compare experimental and observational study designs, and make recommendations for future investigation of drought-induced mortality mechanisms. We found that studies in which physiological processes were measured in both dying trees and in control treatment or surviving

113 trees simultaneously, provided the most insight into mortality physiology. These results were
114 most useful for comparison with other studies, especially for non-structural carbohydrate
115 dynamics. We would also emphasize that studies which assessed physiological processes related
116 to both carbon starvation and hydraulic failure simultaneously were the most effective for
117 investigating these coupled processes. From our synthesis, it is apparent that many recent studies
118 on the physiology of drought-induced tree mortality neglected measurement of hydraulic
119 function (Figure 1A, Supplementary Table 1) to focus on non-structural carbohydrate dynamics
120 (Figure 1B, C, D). Given the recent concern about artifacts in the measurement of xylem
121 hydraulic conductance (Wheeler et al. 2013), we advocate measurement of both water potential
122 and native hydraulic conductivity for quantifying PLC. If water potential is the only
123 measurement possible, such as in an opportunistic study of trees dying in the field from natural
124 drought, these data will be of limited use for inferring hydraulic failure if an appropriate
125 hydraulic vulnerability curve is not available for the species, population, and growth form
126 measured. NSC measurements provide useful information for investigating carbon limitation
127 and starvation in drought-induced mortality, but innovative research that manipulates NSCs in
128 dying trees, explores survival thresholds, and quantifies energy stores in other compounds, such
129 as lipids, are needed. Although assessment of carbon reserves and hydraulic function
130 immediately prior to mortality were the focus of this synthesis, time-series data of physiological
131 function are also informative; e.g., for investigating the effect of antecedent conditions and
132 estimating survival thresholds based on prior drought stress that was not lethal. We further
133 recommend that future studies clearly state the techniques used to define tree death, and trees
134 that were thought to be dead, be re-watered to confirm mortality. In addition to physiological
135 responses, studies should also report data on the environmental drivers (e.g. temperature, relative

136 humidity, vapor pressure deficit, soil moisture content, precipitation) that resulted in tree
137 mortality, because these are an important component for developing a predictive model
138 framework of mortality response.
139
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Supplementary Acknowledgements.

This research was also supported by the National Science Foundation EPSCoR and Hydrological Science programs, and NSF EF-1340624, EF-1550756, EAR-1331408, and IOS-1250650, The U.S. Geological Survey, ERC Advanced Grant (CDREG, 32998), Wyoming Water Development, the Alexander von Humboldt Foundation, the University of California, Santa Cruz, Spanish grants CGL2010-16373 and CGL2013-46808-R, URPP-GCB of the University of Zurich, Forests and Wood Products Australia, ICM (Iniciativa Científica Milenio) P05–002, the University of Delaware, and NSERC Discovery. FIP thanks Fondecyt 1160330. This study has been supported by the TRY initiative on plant traits (http://www.trydb.org). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönisch (Max-Planck-Institute for Biogeochemistry, Jena, Germany). TRY is/has been supported by DIVERSITAS, IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System), the French Foundation for Biodiversity Research (FRB), and GIS "Climat, Environnement et Société" France.

Tables and Figures

Supplementary Table 1. A summary of studies included in the synthesis. Noted are study name, species studied, type of experiment or study, size of tree species, relevant literature, tissue analyzed for non-structural carbohydrates (NSC), which NSC data were available for comparison, and method for determining percent loss of hydraulic conductivity (PLC), either direct measurement, or estimation from plant water potential (Ψ_p) or hydraulic conductivity. Tissues analyzed for NSC included bole, branch, leaf, root, stem, and twig as defined in each study. Numbers before study names correspond to superscripts and notation used in Figures. Footnotes indicate whether data were pooled or treated separately when studies also included temperature or [CO_2] treatments. Data were treated separately for these treatments when factor effects were significant ($p < 0.05$) in ANOVA for NSC or PLC, and pooled when differences were not significant.

Study	Species	Type	Size	Reference	NSC tissues	NSC compared	PLC method
(1) Coyhaique	*Acer pseudoplatanus*	Outdoor potted	Seedling	Piper and Fajardo 2016	Leaf, root, stem	Death vs. control	NA
(2) University of Alberta	*Populus balsamifera, Populus tremuloides*	Greenhouse/ outdoor potted	Seedling	Galvez et al. 2013	Leaf, root, stem	Death vs. control Initial vs. death	Measured directly
(3) San Juan	*Populus tremuloides*	Field	Tree	Anderegg et al. 2012	Branch, leaf, root	Death vs. control	Measured directly
(4) CSIRO Hobart	*Eucalyptus globulus, Eucalyptus smithii, Pinus radiata*	Greenhouse	Seedling	Mitchell et al. 2013, 2014	Leaf, root, stem	Death vs. control Initial vs. death	Estimated from Ψ_p
(5) Hawkesbury Institute for the Environment*	*Eucalyptus radiata*	Greenhouse	Seedling	Duan et al. 2014	Leaf, root, stem	Death vs. control Initial vs. death	Measured directly
(6) Universidad Austral de Chile	*Nothofagus dombeyi, Nothofagus nitida*	Greenhouse	Sapling	Piper 2011	Leaf, root, stem	Death vs. control	NA
(7) Malua	*Dryobalanops lanceolata, Durio oxleyanus, Hopea nervosa, Koompassia excelsa, Parashorea malaanonan, Parashorea tomentella, Shorea argentifolia, Shorea beccariana, Shorea macrophylla, Shorea parvifolia*	Greenhouse	Seedling	O'Brien et al. 2015	Leaf, root, stem	Death vs. control Initial vs. death	NA
(8) Hawkesbury Institute for the Environment #2†	*Callitris rhomboidea, Pinus radiata*	Greenhouse	Seedling	Duan et al. 2015	Leaf, root, stem	Death vs. control Initial vs. death	Measured directly
(9) Cortez	*Juniperus osteosperma, Pinus edulis*	Outdoor potted	Sapling	Anderegg and Anderegg 2013	Branch, leaf, root	Death vs. control Initial vs. death	Measured directly
(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*	Outdoor potted	Sapling	Hartmann et al. 2013a	Leaf, root, stem	Death vs. control Initial vs. death	NA
(11) Max-Planck Institute for Biogeochemistry Jena #2‡	*Picea abies*	Growth chamber	Sapling	Hartmann et al. 2013b	Leaf, root, stem	Death vs. control Initial vs. death	NA
(12) Biosphere 2, University of Arizona§	*Pinus edulis*	Greenhouse	Sapling	Adams et al. 2009; 2013	Leaf	Death vs. control Initial vs. death	Estimated from Ψ_p
(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*	Greenhouse	Sapling	Sevanto et al. 2014	Leaf, twig	Death vs. control Initial vs. death	Estimated from Ψ_p
(14) Sevilleta	*Pinus edulis*	Field	Tree	Plaut et al. 2012; Dickman et al. 2015; McDowell et al. 2016	Leaf, twig	Death vs. control Initial vs. death	Modeled from hydraulic conductance
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*	Greenhouse	Sapling	Garcia Forner et al. 2016b	Branch, root, stem	Death vs. control Initial vs. death	NA
(16) CREAF – Soriguera	*Pinus sylvestris*	Field	Tree	Galiano et al. 2011	Bole	Death vs. control	NA
(17) Mesita del Buey	*Pinus edulis*	Field	Tree	Breshears et al. 2005; 2009	NA	NA	Estimated from Ψ_p
(18) University of Sheffield¶	*Sequoia sempervirens*	Growth chamber	Sapling	Quirk et al. 2013	Leaf, root	Initial vs. death	Measured directly
(19) Idaho State University	*Pinus flexilis*	Outdoor planted	Seedling	Reinhardt et al. 2015	Root, shoot	Initial vs. death	NA

316 *NSC data were pooled for 400 and 640 ppm [CO_2] treatments, but treated separately for 26°C and 30°C temperature treatments; PLC

317 data were pooled across all [CO_2] and temperature treatments.

318 †Data were pooled for 26°C and 30°C temperature treatments, but treated separately for 400 and 640 ppm [CO_2] treatments

319 ‡Data were treated separately for ambient (400 ppm) and low (20-75 ppm) [CO_2] treatments.

320 §Data were pooled for ambient and +4°C temperature treatments.

321 ¶Data included were for the 200ppm [CO_2] treatment only, as the other drought and [CO_2] treatments did not cause mortality.

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Supplementary Table 2. Plant size and age data available for each case (species × study combination) included in this synthesis. Means and standard errors are provided for the sample population for plant height, dry biomass, diameter at the root collar (DRC), and diameter at breast height (DBH).

Study	Species	Age	Size descriptor	Height (mean)	(cm) (s.e.)	Biomass (mean)	(g) (s.e.)	DRC (mean)	(cm) (s.e.)	DBH (mean)	(cm) (s.e.)
(1) Coyhaique	*Acer pseudoplatanus*	3 months	Seedling	13.28	3.88	0.186	0.01 g				
(2) University of Alberta	*Populus balsamifera*	1 year	Seedling	29.65	2.13						
(2) University of Alberta	*Populus tremuloides*	1 year	Seedling	62.12	2.97						
(3) San Juan	*Populus tremuloides*	90 years	Tree	1500						24	
(4) CSIRO Hobart	*Eucalyptus globulus*	6 months	Seedling	61.4	1.9	176.2	1.3	0.51	0.015		
(4) CSIRO Hobart	*Eucalyptus smithii*	6 months	Seedling	53.1	3.7	89.1	1.4	0.37	0.016		
(4) CSIRO Hobart	*Pinus radiata*	18 months	Seedling	66.3	1.9	562	4.5	1.14	0.045		
(5) Hawkesbury Institute for the Environment	*Eucalyptus radiata*	5 months	Seedling	58.8	0.7	7.5	1.0	0.42	0.01		
(6) Universidad Austral de Chile	*Nothofagus dombeyi*	2.5 years	Sapling	22.5	1.45	3.0	0.32				
(6) Universidad Austral de Chile	*Nothofagus nitida*	2.5 years	Sapling	32.1	1.65	5.2	0.38				
(7) Malua	*Dryobalanops lanceolata*	4 months	Seedling	32.6	0.6	2.0	0.35	0.34	0.005		
(7) Malua	*Durio oxleyanus*	4 months	Seedling	46.2	1.0	3.9	0.41	1.1	0.018		
(7) Malua	*Hopea nervosa*	4 months	Seedling	18.2	0.4	0.7	0.08	0.20	0.004		
(7) Malua	*Koompassia excelsa*	4 months	Seedling	22.7	0.4	0.5	0.05	0.21	0.003		
(7) Malua	*Parashorea malaanonan*	4 months	Seedling	16.1	0.5	0.8	0.13	0.21	0.005		
(7) Malua	*Parashorea tomentella*	4 months	Seedling	20.0	0.4	1.1	0.09	0.26	0.005		
(7) Malua	*Shorea argentifolia*	4 months	Seedling	17.4	0.3	0.5	0.02	0.18	0.003		
(7) Malua	*Shorea beccariana*	4 months	Seedling	13.8	0.3	0.7	0.07	0.22	0.005		
(7) Malua	*Shorea macrophylla*	4 months	Seedling	48.6	1.1	6.5	0.97	0.6	0.01		
(7) Malua	*Shorea parvifolia*	4 months	Seedling	18.6	0.3	0.5	0.06	0.21	0.004		
(8) Hawkesbury Institute for the Environment #2	*Callitris rhomboidea*	5 months	Seedling	19.4	0.48	1.07	0.2	1.7	0.04		
(8) Hawkesbury Institute for the Environment #2	*Pinus radiata*	5 months	Seedling	28.8	0.36	2.59	0.3	3.4	0.04		
(9) Cortez	*Juniperus osteosperma*	10 years	Sapling	50				1.0			
(9) Cortez	*Pinus edulis*	3 years	Sapling	150				4.0			
(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*	7 years	Sapling	150				6.5			
(11) Max-Planck Institute for Biogeochemistry Jena #2	*Picea abies*	4 years	Sapling	75		106	13.0				
(12) Biosphere 2, University of Arizona	*Pinus edulis*	15-20 years	Sapling	177	7			6.7	0.36		

(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*	20-40 years	Sapling	200			5.29	1.02		
(14) Sevilleta	*Pinus edulis*	60-150 years	Tree	432	80		22.74	0.84		
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*	6 years	Sapling	150	30		2.7	0.6		
(16) CREAF – Soriguera	*Pinus sylvestris*	69 yrs	Tree	1140	270				24.7	0.85
(17) Mesita del Buey	*Pinus edulis*	100-150 years	Tree	580	78		27.0	3.7		
(18) University of Sheffield	*Sequoia sempervirens*	1 year	Sapling	37	10		3.5	0.17		
(19) Idaho State University	*Pinus flexilis*	2 weeks	Seedling	5.0		0.02	0.15			

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328 **Supplementary Table 3.** Methods used in the determination of plant death for each study included in this synthesis**.**

Study	Species	100% brown foliage	90% brown foliage	No growth/ survival with re-watering	No detectable respiration	Neutral red stain	Lack of green cambium
(1) Coyhaique	*Acer pseudoplatanus*	X					X
(2) University of Alberta	*Populus balsamifera, Populus tremuloides*	X		X			X
(3) San Juan	*Populus tremuloides*	X					X
(4) CSIRO Hobart	*Eucalyptus globulus, Eucalyptus smithii, Pinus radiata*	X		X	X		
(5) Hawkesbury Institute for the Environment	*Eucalyptus radiata*	X			X		
(6) Universidad Austral de Chile	*Nothofagus dombeyi, Nothofagus nitida*		X	X			
(7) Malua	*Dryobalanops lanceolata, Durio oxleyanus, Hopea nervosa, Koompassia excelsa, Parashorea malaanonan, Parashorea tomentella, Shorea argentifolia, Shorea beccariana, Shorea macrophylla, Shorea parvifolia*			X			X
(8) Hawkesbury Institute for the Environment #2	*Callitris rhomboidea, Pinus radiata*	X			X		
(9) Cortez	*Juniperus osteosperma, Pinus edulis*	X		X			
(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*	X			X		X
(11) Max-Planck Institute for Biogeochemistry Jena #2	*Picea abies*	X			X		X
(12) Biosphere 2, University of Arizona	*Pinus edulis*		X	X			
(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*			X	X	X	
(14) Sevilleta	*Pinus edulis*	X					
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*	X		X			X
(16) CREAF – Soriguera	*Pinus sylvestris*	X					
(17) Mesita del Buey	*Pinus edulis*		X				
(18) University of Sheffield	*Sequoia sempervirens*				X		
(19) Idaho State University	*Pinus flexilis*	X		X	X		

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Supplementary Table 4. Sample size for PLC and NSC data shown in Figure 1 and Supplementary Figure 1 for each case and tissue. Sample sizes are shown for dying (D) and ambient moisture, watered control, or surviving (C) trees. For values marked with an asterisk, only means and standard error were available for synthesis. For some cases where only means and standard error were available, sample sizes were not available, as indicated with "NA".

		PLC		Leaf NSC		Root NSC		Stem/ Twig NSC		Bole NSC		Branch NSC	
Study	**Species**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	**C**	**D**	**C**
(1) Coyhaique	*Acer pseudoplatanus*			15	20	16	20	16	20				
(2) University of Alberta	*Populus balsamifera*	6*	6*	6	6	4	4	4	4				
(2) University of Alberta	*Populus tremuloides*	6*	6*	6	6	4	4	4	4				
(3) San Juan	*Populus tremuloides*	6	6	NA*	NA*	NA*	NA*					NA*	NA*
(4) CSIRO Hobart	*Eucalyptus globulus*	3	3	6	6	6	6	6	6				
(4) CSIRO Hobart	*Eucalyptus smithii*			6	6	6	6	5	5				
(4) CSIRO Hobart	*Pinus radiata*			6	6	6	6	6	6				
(5) Hawkesbury Institute for the Environment (ambient temp.)	*Eucalyptus radiata*	3*		8	6	8	6	8	6				
(5) Hawkesbury Institute for the Environment (+4°C)	*Eucalyptus radiata*	3*		8	6	8	6	8	6				
(6) Universidad Austral de Chile	*Nothofagus dombeyi*			8	8	8	8	8	8				
(6) Universidad Austral de Chile	*Nothofagus nitida*			8	7	8	8	8	8				
(7) Malua	*Dryobalanops lanceolata*			4	3	4	3	4	3				
(7) Malua	*Durio oxleyanus*			3	1	3	1	3	1				
(7) Malua	*Hopea nervosa*			3	3	3	3	3	3				
(7) Malua	*Koompassia excelsa*			4	3	4	3	4	3				
(7) Malua	*Parashorea malaanonan*			3	3	3	3	3	3				
(7) Malua	*Parashorea tomentella*			3	3	3	3	3	3				
(7) Malua	*Shorea argentifolia*			4	3	4	3	4	3				
(7) Malua	*Shorea beccariana*			3	3	3	3	3	3				
(7) Malua	*Shorea macrophylla*			3	3	3	3	3	3				
(7) Malua	*Shorea parvifolia*			4	3	4	3	4	3				
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Callitris rhomboidea*	3*		8	8	8	8	8	8				

(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Callitris rhomboidea*	3*		8	8	8	7	8	8				
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Pinus radiata*	3*		8	8	8	8	8	8				
(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Pinus radiata*	3*		8	8	8	8	8	8				
(9) Cortez	*Juniperus osteosperma*	4*	4*	3*	3*	3*	3*					3*	3*
(9) Cortez	*Pinus edulis*	4*	4*	3*	3*	3*	3*					3*	3*
(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*			4	6	4	6					4	6
(11) Max-Planck Institute for Biogeochemistry Jena #2 (ambient CO_2)	*Picea abies*			6	6	6	8					6	5
(11) Max-Planck Institute for Biogeochemistry Jena #2 (low CO_2)	*Picea abies*			6	6	6	6					6	5
(12) Biosphere 2, University of Arizona	*Pinus edulis*	9	9	8	9								
(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*	4	4	4	5			4	5				
(14) Sevilleta	*Pinus edulis*	3	3	9	5			9	5				
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*			10	10	10	10					10	9
(16) CREAF – Soriguera	*Pinus sylvestris*									4	38		
(17) Mesita del Buey	*Pinus edulis*	7	7										
(18) University of Sheffield	*Sequoia sempervirens*	4	4										

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Supplementary Table 5. Sample size for NSC data shown in Supplementary Figure 6 for each case and tissue. Sample sizes are shown for drought trees initially (I) and at or near-death (D). For values marked with an asterisk, only means and standard error were available for synthesis.

		Leaf		Root		Stem/ Twig		Branch	
Study	**Species**	**I**	**D**	**I**	**D**	**I**	**D**	**I**	**D**
(2) University of Alberta	*Populus balsamifera*	6	6	6	4	6	4		
(2) University of Alberta	*Populus tremuloides*	6	6	6	4	6	4		
(4) CSIRO Hobart	*Eucalyptus globulus*	6	6	6	6	6	6		
(4) CSIRO Hobart	*Eucalyptus smithii*	6	6	6	6	6	5		
(4) CSIRO Hobart	*Pinus radiata*	6	6	6	6	6	6		
(5) Hawkesbury Institute for the Environment (ambient temp.)	*Eucalyptus radiata*	6	8	6	8	6	8		
(5) Hawkesbury Institute for the Environment (+4°C)	*Eucalyptus radiata*	6	8	6	8	6	8		
(7) Malua	*Dryobalanops lanceolata*	3	4	3	4	3	4		
(7) Malua	*Durio oxleyanus*	3	3	3	3	3	3		
(7) Malua	*Hopea nervosa*	3	3	3	3	3	3		
(7) Malua	*Koompassia excelsa*	3	4	3	4	3	4		
(7) Malua	*Parashorea malaanonan*	4	3	4	3	4	3		
(7) Malua	*Parashorea tomentella*	3	3	3	3	3	3		
(7) Malua	*Shorea argentifolia*	3	4	3	4	3	4		
(7) Malua	*Shorea beccariana*	3	3	3	3	3	3		
(7) Malua	*Shorea macrophylla*	3	3	3	3	3	3		
(7) Malua	*Shorea parvifolia*	3	4	3	4	3	4		
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Callitris rhomboidea*	6	8	6	8	4	8		
(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Callitris rhomboidea*	6	8	6	8	6	8		
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Pinus radiata*	6	8	6	8	6	8		
(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Pinus radiata*	6	8	6	8	6	8		
(9) Cortez	*Juniperus osteosperma*	3*	3*	3*	3*			3*	3*
(9) Cortez	*Pinus edulis*	3*	3*	3*	3*			3*	3*

(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*	4	4	4	4				4	4
(11) Max-Planck Institute for Biogeochemistry Jena #2 (ambient CO_2)	*Picea abies*	6	6	6	6				5	6
(11) Max-Planck Institute for Biogeochemistry Jena #2 (low CO_2)	*Picea abies*	6	6	6	6				6	6
(12) Biosphere 2, University of Arizona	*Pinus edulis*	9	8							
(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*	4	4			4	4			
(14) Sevilleta	*Pinus edulis*	5	9							
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*								4	10
(18) University of Sheffield	*Sequoia sempervirens*	4	4			4	4			
(19) Idaho State University	*Pinus flexilis*	7	25			3	12			

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Supplementary Table 6. Hydraulic data used to estimate percent loss of hydraulic conductivity from water potential data (Figure 1A), and in the analysis of relationships between functional traits and non-structural carbohydrate response at mortality (Figure 2). Hydraulic traits are shown for water potential point of 50% embolism (Ψ_{50}), hydraulic safety margin (Ψ_{50} –minimum Ψ), and the embolism entry point (Ψ_e) Hydraulic trait data were unavailable for *Eucalyptus radiata*, *Eucalyptus smithii*, *Nothofagus nitida*, and all ten tropical species in study 7 (Supplementary Table 1).

Species	Study	Taxonomic Group	Ψ_{50} (MPa)	Safety Margin (MPa)	Ψ_e (MPa)	Sources
Acer pseudoplatanus	1	Angiosperm	-1.66	0.51	-1.31	Khalil and Grace 1992; Tissier et al. 2004; Choat et al. 2012
Eucalyptus globulus	4	Angiosperm	-5.62	3.32	-3.87	Zeppel et al., unpublished data
Nothofagus dombeyi	6	Angiosperm	-3.78	2.40	-2.10	Piper 2011; Bucci et al. 2012
Populus balsamifera	2	Angiosperm	-1.80	1.10	-0.74	Hacke and Sauter 1995; Choat et al. 2012
Populus tremuloides	2,3	Angiosperm	-2.74	0.73	-0.72	Sperry and Sullivan 1992; Choat et al. 2012
Callitris rhomboidea	8	Gymnosperm	-9.67	6.27	-7.24	Brodribb and Cochard 2009; Choat et al. 2012
Juniperus osteosperma	9	Gymnosperm	-6.92	3.46	-4.54	Linton et al. 1998; Choat et al. 2012
Picea abies	10, 11	Gymnosperm	-3.98	-0.36	-3.82	Mayr et al. 2003; Choat et al. 2012
Pinus edulis	9	Gymnosperm	-4.59	2.32	-2.52	Linton et al. 1998; Choat et al. 2012; Garcia-Forner et al. 2016a; Hudson et al., unpublished data
Pinus edulis	12	Gymnosperm	-4.45	2.02	-2.00	Garcia-Forner et al. 2016a; Hudson et al., unpublished data
Pinus edulis	13	Gymnosperm	-4.45	2.18	-2.00	Choat et al. 2012; Garcia-Forner et al. 2016a; Hudson et al., unpublished data
Pinus edulis	14	Gymnosperm	-4.50	2.10	-2.24	Choat et al. 2012; Hudson et al., unpublished data
Pinus edulis	17	Gymnosperm	-4.39	1.54	-1.76	Garcia-Forner et al. 2016a
Pinus radiata	4, 8	Gymnosperm	-4.31	1.06	-1.91	Zeppel et al., unpublished data
Pinus sylvestris	15, 16	Gymnosperm	-3.29	1.01	-1.71	Martínez-Vilalta et al. 2009; Choat et al. 2012

Supplementary Table 7. A comparison of non-structural carbohydrate responses between the two types of data normalization used in the synthesis, percent deviation from control at- or near-mortality (Dev; Figure 1b-d) and percent change from initial, pre-drought measurements to at or near-mortality assessment (Chg; Supplementary Figure 6). Means are shown for each tissue measured in each case for which both types of data were available.

		Leaf		Root		Stem/ Twig		Branch	
Study	**Species**	**Dev**	**Chg**	**Dev**	**Chg**	**Dev**	**Chg**	**Dev**	**Chg**
(2) University of Alberta	*Populus balsamifera*	-33.4	40.8	-53.0	150.8	-29.6	85.0		
(2) University of Alberta	*Populus tremuloides*	-19.5	27.0	-70.4	-14.9	-41.9	20.6		
(4) CSIRO Hobart	*Eucalyptus globulus*	33.0	23.8	-27.5	23.1	-11.0	1.2		
(4) CSIRO Hobart	*Eucalyptus smithii*	-15.1	-5.6	-37.5	29.6	2.9	5.4		
(4) CSIRO Hobart	*Pinus radiata*	-47.9	-37.3	-24.9	24.3	-49.7	-34.1		
(5) Hawkesbury Institute for the Environment (ambient temp.)	*Eucalyptus radiata*	-20.7	-0.2	-27.0	-33.6	-42.6	-4.1		
(5) Hawkesbury Institute for the Environment (+4°C)	*Eucalyptus radiata*	-58.4	0.9	-35.6	-41.3	-48.3	-29.8		
(7) Malua	*Dryobalanops lanceolata*	19.0	-15.0	1.8	-15.1	-2.3	-1.9		
(7) Malua	*Durio oxleyanus*	-32.5	-38.6	-9.8	-3.8	10.4	26.6		
(7) Malua	*Hopea nervosa*	25.9	31.1	29.2	114.9	39.3	38.8		
(7) Malua	*Koompassia excelsa*	-21.1	-3.7	80.2	71.2	143.1	84.7		
(7) Malua	*Parashorea malaanonan*	-14.3	-36.7	29.8	-30.5	73.5	80.3		
(7) Malua	*Parashorea tomentella*	2.7	19.8	158.2	166.3	189.0	198.8		
(7) Malua	*Shorea argentifolia*	-10.7	-8.9	39.7	-21.0	-15.8	30.3		
(7) Malua	*Shorea beccariana*	-15.4	-30.0	90.6	8.9	7.6	-16.7		
(7) Malua	*Shorea macrophylla*	-25.2	-5.0	26.9	-37.3	38.3	68.3		
(7) Malua	*Shorea parvifolia*	-16.1	-20.4	43.4	16.6	-48.2	-53.7		
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Callitris rhomboidea*	5.7	101.5	-13.8	-4.4	97.7	43.9		
(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Callitris rhomboidea*	-2.6	103.4	-23.5	12.9	75.0	40.9		
(8) Hawkesbury Institute for the Environment #2 (ambient CO_2)	*Pinus radiata*	4.8	13.2	-9.3	54.1	-12.5	-20.3		

(8) Hawkesbury Institute for the Environment #2 (high CO_2)	*Pinus radiata*	-21.6	14.7	11.1	154.2	-1.8	-8.0		
(9) Cortez	*Juniperus osteosperma*	-2.1	1.7	-27.9	-38.4			23.5	-20.7
(9) Cortez	*Pinus edulis*	-24.2	4.7	-33.1	-26.8			-34.9	-53.7
(10) Max-Planck Institute for Biogeochemistry Jena #1	*Picea abies*	-0.6	29.3	-76.9	-52.7			-14.5	-4.4
(11) Max-Planck Institute for Biogeochemistry Jena #2 (ambient CO_2)	*Picea abies*	-34.7	13.9	-62.3	-53.9			-19.1	-18.4
(11) Max-Planck Institute for Biogeochemistry Jena #2 (low CO_2)	*Picea abies*	-58.9	-34.9	-94.7	-93.2			-66.0	-67.6
(12) Biosphere 2, University of Arizona	*Pinus edulis*	-50.9	-30.0						
(13) Los Alamos National Laboratory Greenhouse	*Pinus edulis*	-47.6	-30.2			-55.3	-56.6		
(14) Sevilleta	*Pinus edulis*	-38.3	-26.9						
(15) CREAF – IRTA, Barcelona	*Pinus sylvestris*							-71.8	-79.3

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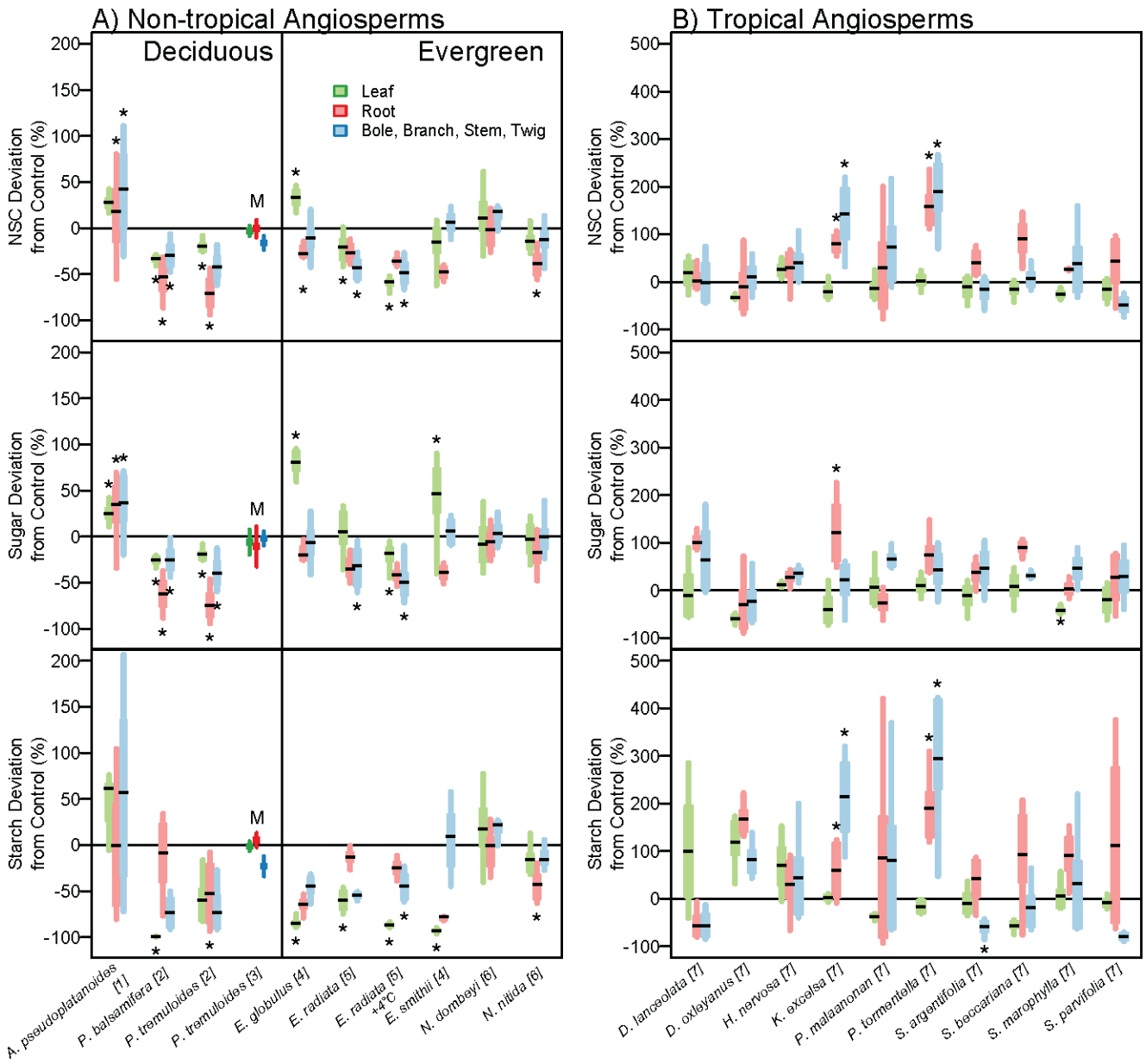
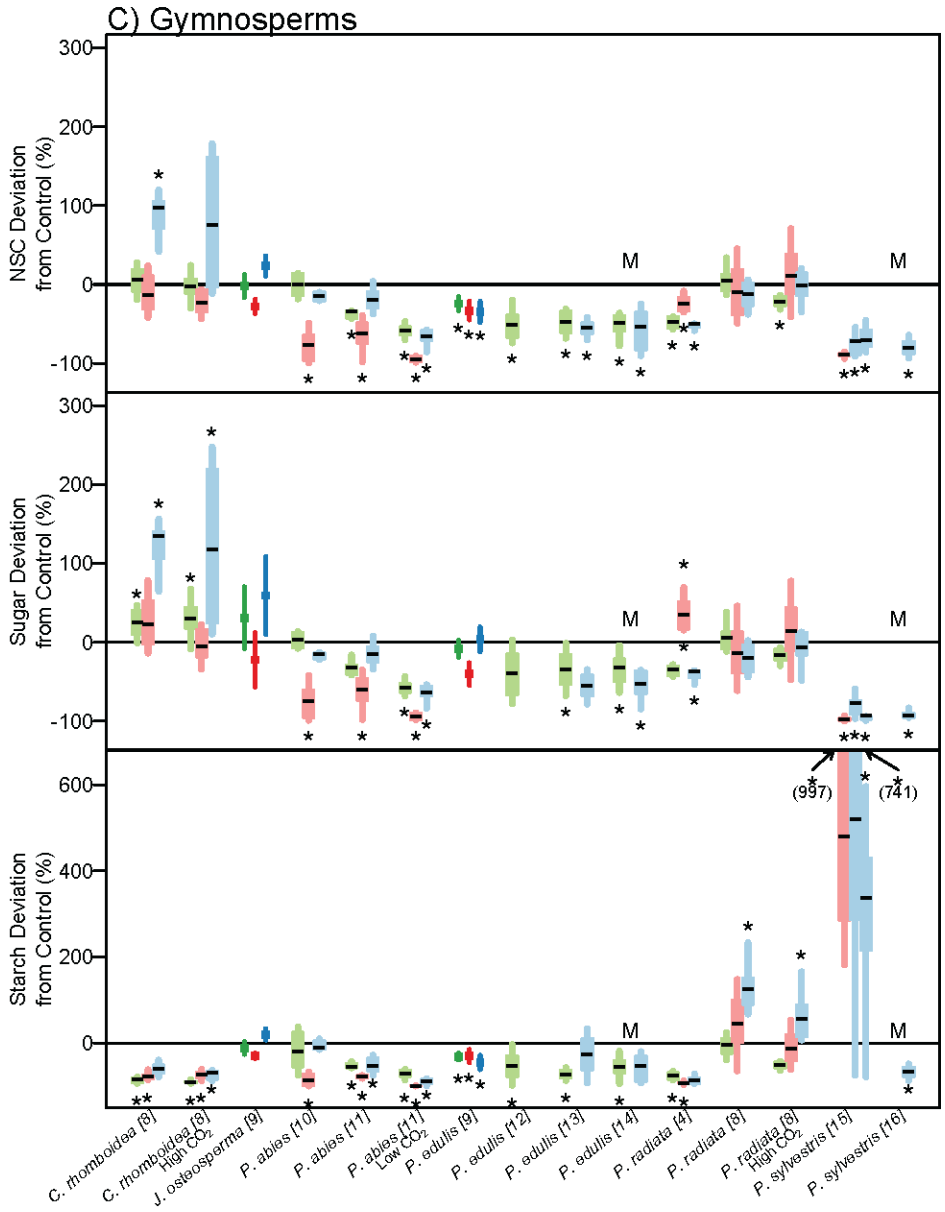
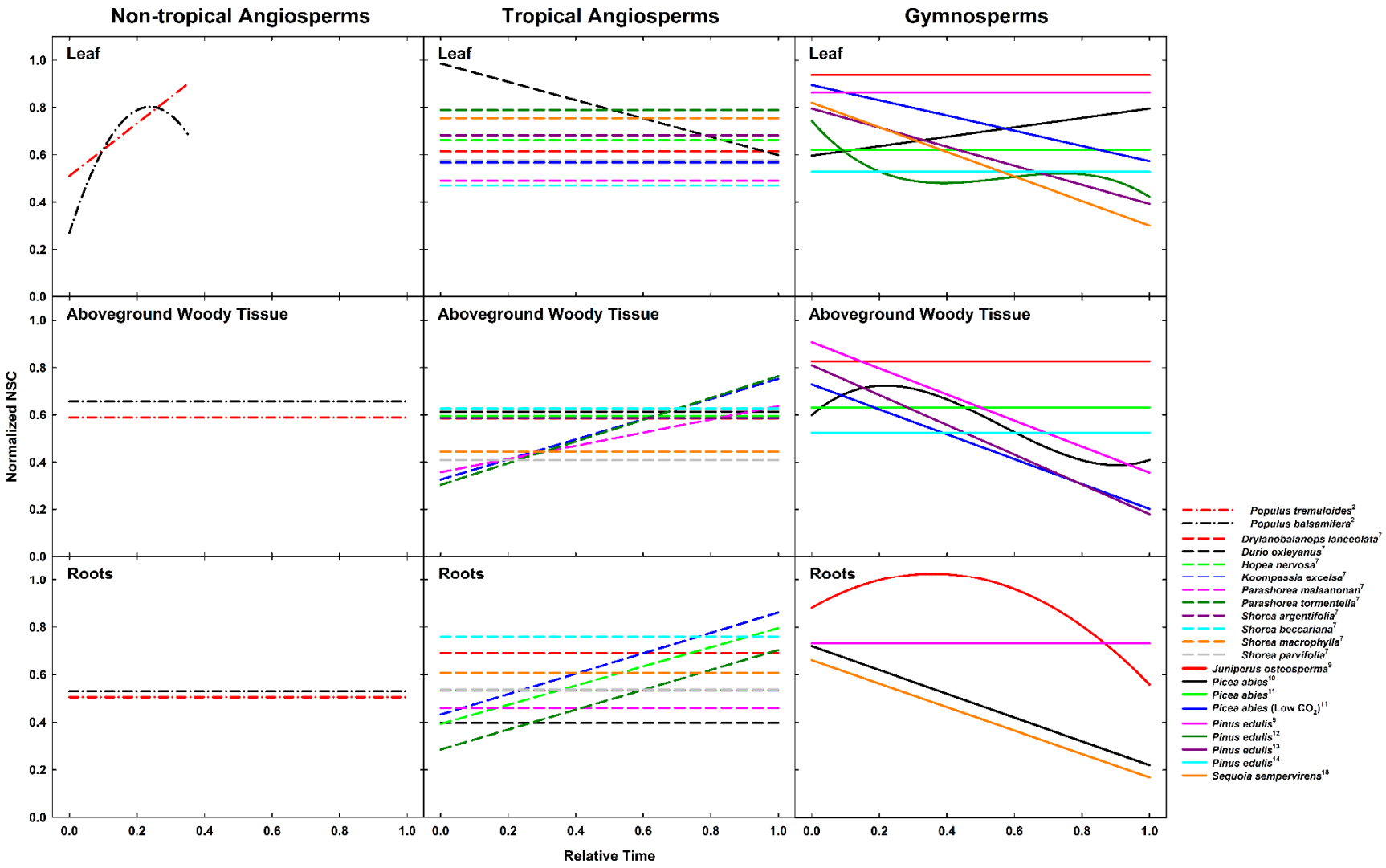

A) Non-tropical Angiosperms
B) Tropical Angiosperms
Deciduous
Evergreen
Leaf
Root
Bole, Branch, Stem, Twig
NSC Deviation from Control (%)
Sugar Deviation from Control (%)
Starch Deviation from Control (%)
M
A. pseudoplatanoides [1]
P. balsamifera [2]
P. tremuloides [2]
P. tremuloides [3]
E. globulus [4]
E. radiata [5]
E. radiata [5] +4°C
E. smithii [4]
N. dombeyi [6]
N. nitida [6]
D. lanceolata [7]
D. oxleyanus [7]
H. nervosa [7]
K. excelsa [7]
P. malaanonan [7]
P. tormentella [7]
S. argentifolia [7]
S. beccariana [7]
S. macrophylla [7]
S. parvifolia [7]


C) Gymnosperms
NSC Deviation from Control (%)
Sugar Deviation from Control (%)
Starch Deviation from Control (%)
300
200
100
0
-100
600
400
M
(997)
(741)
C. rhomboidea [8]
C. rhomboidea [8] High CO2
J. osteosperma [9]
P. abies [10]
P. abies [11]
P. abies [11] Low CO2
P. edulis [9]
P. edulis [12]
P. edulis [13]
P. edulis [14]
P. radiata [4]
P. radiata [8]
P. radiata [8] High CO2
P. sylvestris [15]
P. sylvestris [16]

Supplementary Figure 1. Non-structural carbohydrate (NSC) responses at or prior to mortality from drought for total NSC, sugars, and starch, normalized as percent deviation from surviving or control trees for each species in each study. Data are shown separately for deciduous and evergreen non-tropical (temperate and boreal) angiosperm (A), evergreen tropical angiosperm (B), and evergreen gymnosperm (C) species. In all panels for cases where individual data were available, boxes indicate the 25% and 75% quartiles, whiskers indicate the extent of data, and black bars indicate the mean. For cases where only means and a measure of variability were available, means are indicated with squares and error bars are one standard error. Differences for each tissue between drought trees at mortality and ambient, control, or surviving trees are indicated with an asterisk ($p < 0.05$, ANOVA). Numbers after species names designate original studies (Supplementary Table 1). The symbol "M" indicates data from a study on mature trees; all other data are from studies of seedlings, saplings, and small trees (Supplementary Table 1). Sample size for all data analyzed for Figure 1 are shown in Supplementary Table 4.


Non-tropical Angiosperms
Tropical Angiosperms
Gymnosperms
Leaf
Aboveground Woody Tissue
Roots
Normalized NSC
Relative Time
0.0
0.2
0.4
0.6
0.8
1.0
Populus tremuloides[2]
Populus balsamifera[2]
Drylanobalanops lanceolata[7]
Durio oxleyanus[7]
Hopea nervosa[7]
Koompassia excelsa[7]
Parashorea malaanonan[7]
Parashorea tomentella[7]
Shorea argentifolia[7]
Shorea beccariana[7]
Shorea macrophylla[7]
Shorea parvifolia[7]
Juniperus osteosperma[9]
Picea abies[10]
Picea abies[11]
Picea abies (Low CO2)[11]
Pinus edulis[9]
Pinus edulis[12]
Pinus edulis[13]
Pinus edulis[14]
Sequoia sempervirens[18]

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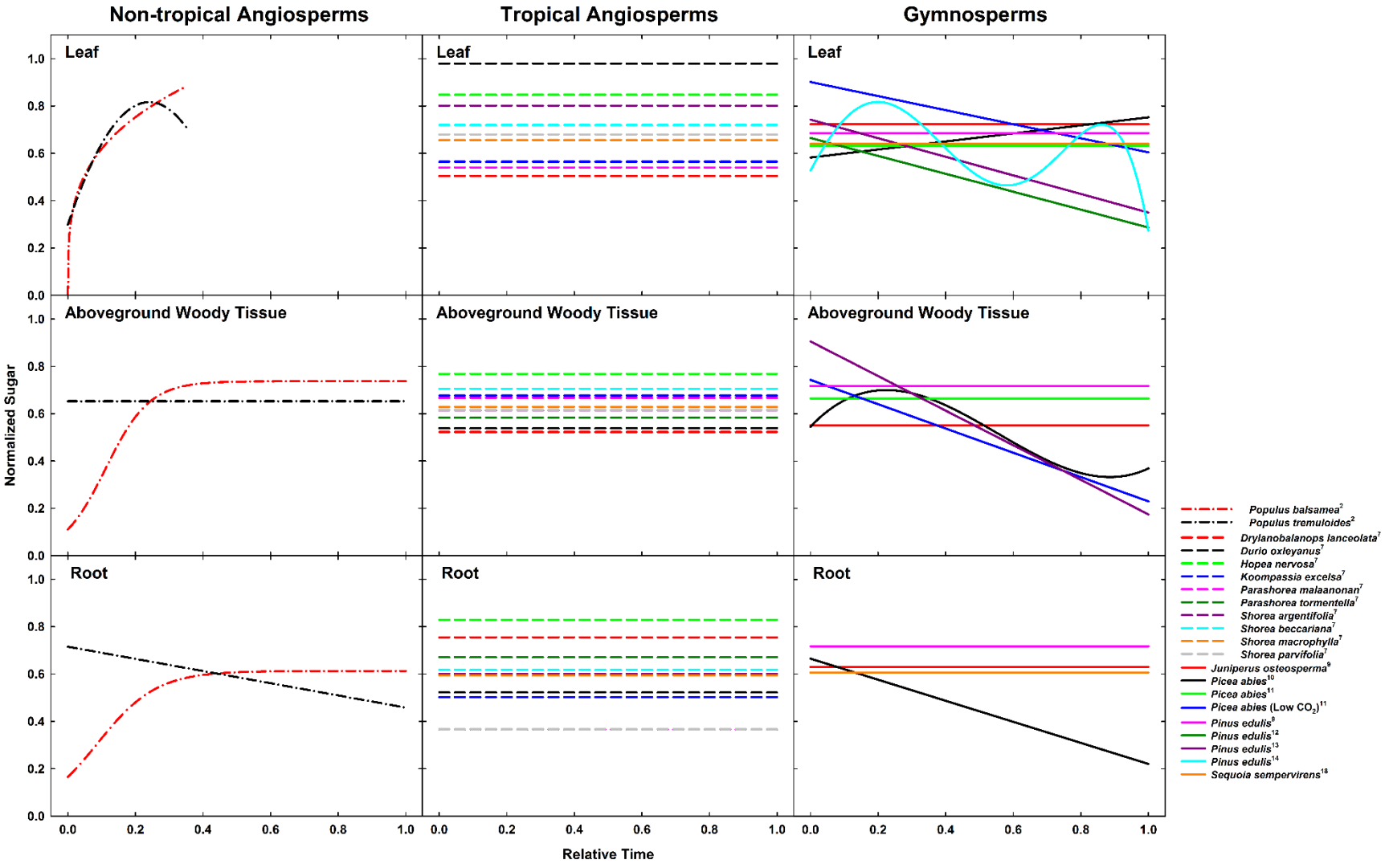
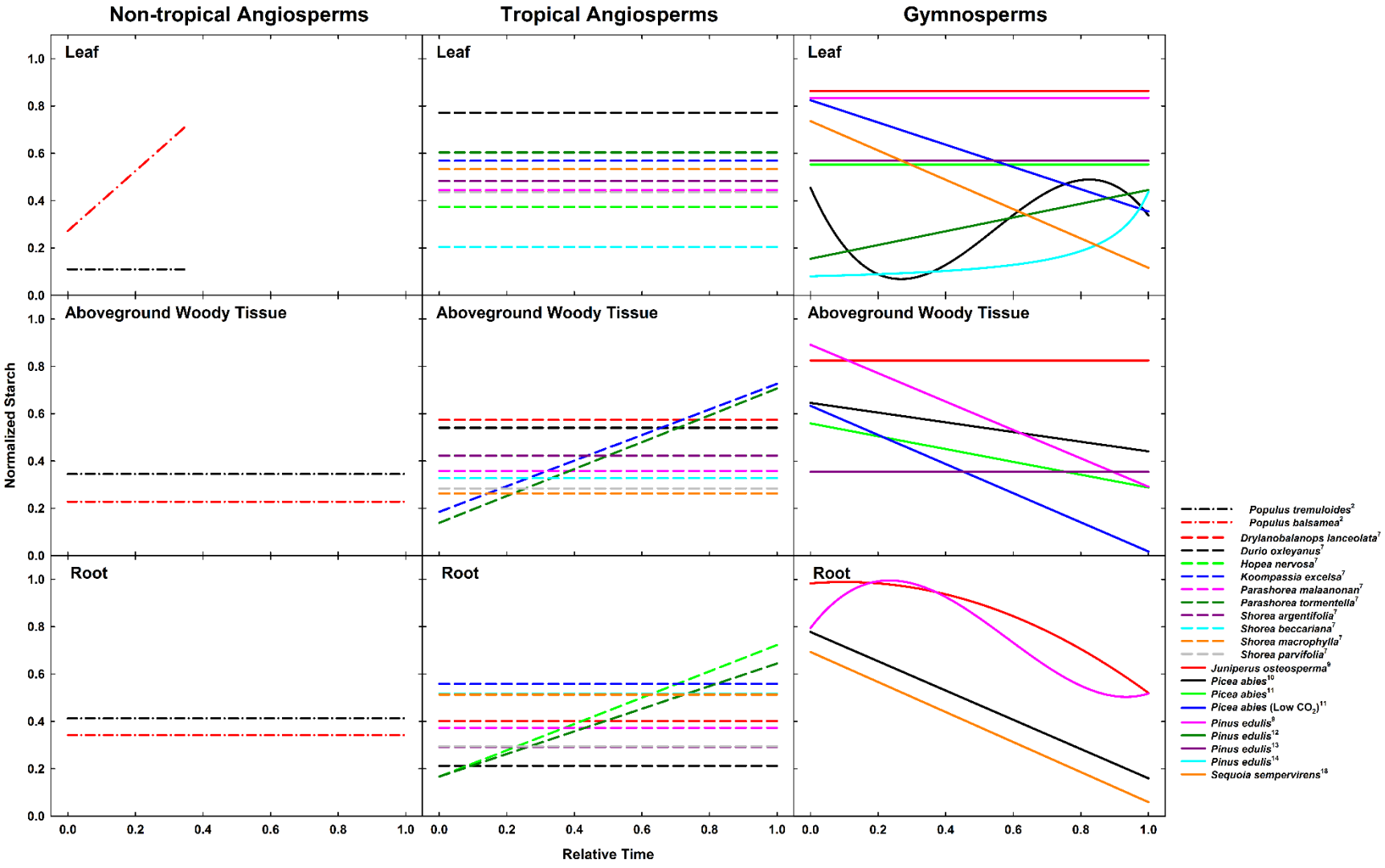
Supplementary Figure 2. Trends in total NSC during drought through mortality in tissues of non-tropical angiosperm, tropical angiosperm, and gymnosperm species. NSC concentrations were normalized in this assessment relative to maximum values for each tissue-specific time series, and are displayed as regression fits for ease of data comparison among multiple studies. Time was also normalized from start of the experiment to the point of tree mortality. Curves cease before the end of the experiment for leaf tissues of *Populus balsamifera* and *Populus tremuloides* as leaf abscission occurred in these species at relative time = ~0.35.


Non-tropical Angiosperms
Tropical Angiosperms
Gymnosperms
Leaf
Aboveground Woody Tissue
Root
Normalized Sugar
Relative Time
0.0
0.2
0.4
0.6
0.8
1.0
Populus balsamea[2]
Populus tremuloides[2]
Drylanobalanops lanceolata[7]
Durio oxleyanus[7]
Hopea nervosa[7]
Koompassia excelsa[7]
Parashorea malaanonan[7]
Parashorea tomentella[7]
Shorea argentifolia[7]
Shorea beccariana[7]
Shorea macrophylla[7]
Shorea parvifolia[7]
Juniperus osteosperma[9]
Picea abies[10]
Picea abies[11]
Picea abies (Low CO2)[11]
Pinus edulis[8]
Pinus edulis[12]
Pinus edulis[13]
Pinus edulis[14]
Sequoia sempervirens[18]

Supplementary Figure 3. Trends in sugar during drought through mortality in tissues of non-tropical angiosperm, tropical angiosperm, and gymnosperm species. Sugar concentrations were normalized in this assessment relative to maximum values for each tissue-specific time series, and are displayed as regression fits for ease of data comparison among multiple studies. Time was also normalized from start of the experiment to the point of tree mortality. Curves cease before the end of the experiment for leaf tissues of *Populus balsamifera* and *Populus tremuloides* as leaf abscission occurred in these species at relative time = ~0.35.


Non-tropical Angiosperms
Tropical Angiosperms
Gymnosperms
Leaf
Aboveground Woody Tissue
Root
Normalized Starch
Relative Time
0.0
0.2
0.4
0.6
0.8
1.0
Populus tremuloides[2]
Populus balsamea[2]
Drylanobalanops lanceolata[7]
Durio oxleyanus[7]
Hopea nervosa[7]
Koompassia excelsa[7]
Parashorea malaanonan[7]
Parashorea tormentella[7]
Shorea argentifolia[7]
Shorea beccariana[7]
Shorea macrophylla[7]
Shorea parvifolia[7]
Juniperus osteosperma[9]
Picea abies[10]
Picea abies[11]
Picea abies (Low CO2)[11]
Pinus edulis[8]
Pinus edulis[12]
Pinus edulis[13]
Pinus edulis[14]
Sequoia sempervirens[18]

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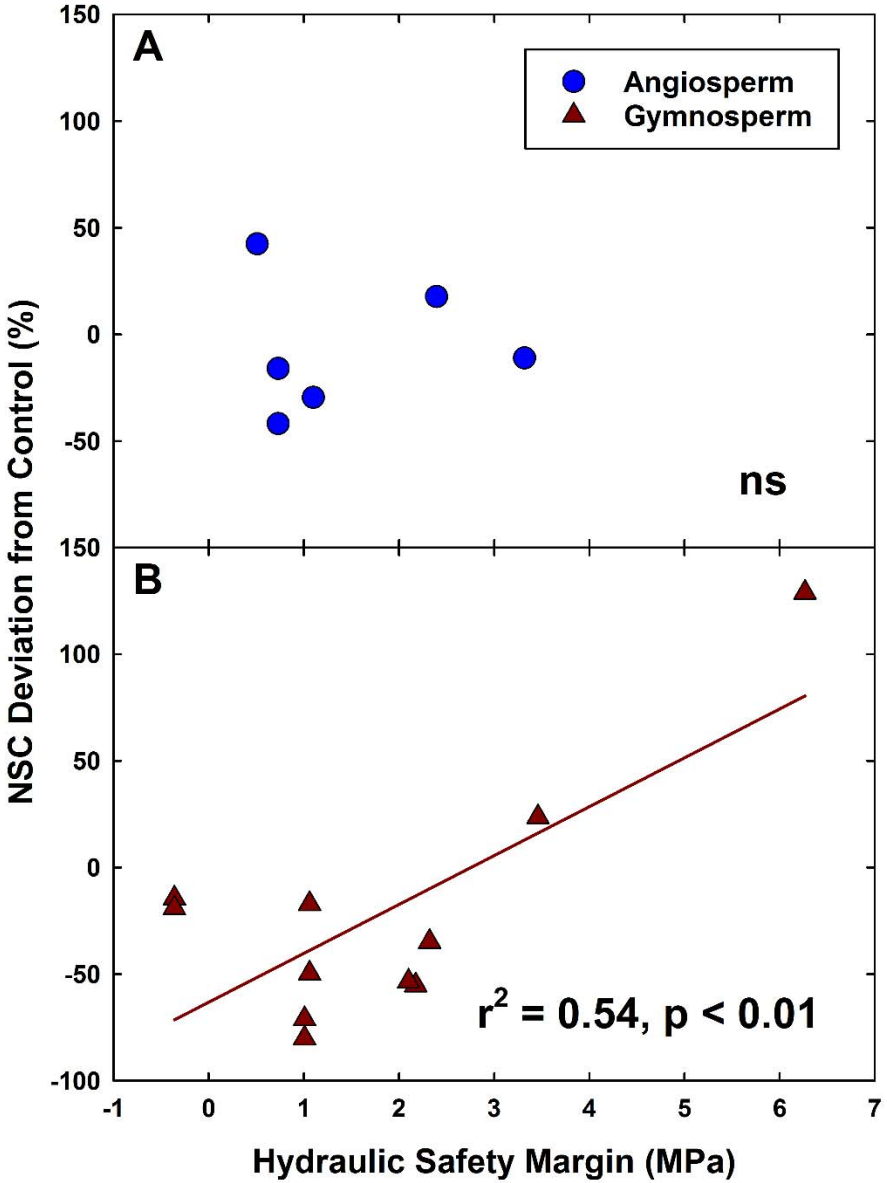
Supplementary Figure 4. Trends in starch during drought through mortality in tissues of non-tropical angiosperm, tropical angiosperm, and gymnosperm species. Starch concentrations were normalized in this assessment relative to maximum values for each tissue-specific time series, and are displayed as regression fits for ease of data comparison among multiple studies. Time was also normalized from the start of the experiment to the point of tree mortality. Curves cease before the end of the experiment for leaf tissues of *Populus balsamifera* and *Populus tremuloides* as leaf abscission occurred in these species at relative time = ~0.35.


A
Angiosperm
Gymnosperm
ns
B
r^2 = 0.54, p < 0.01
NSC Deviation from Control (%)
Hydraulic Safety Margin (MPa)
150
100
50
0
-50
-100
-1
0
1
2
3
4
5
6
7

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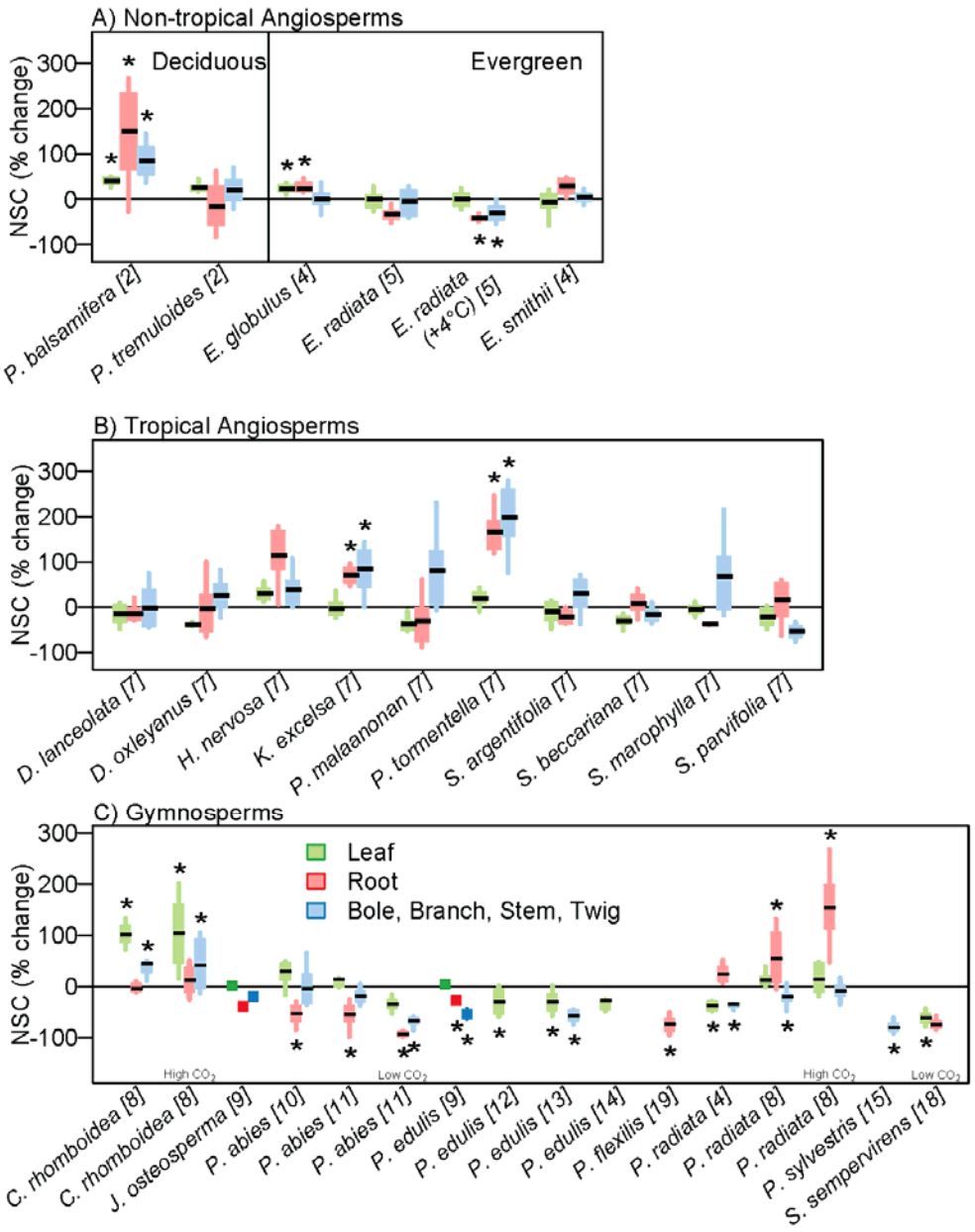
Supplementary Figure 5. The relationship between the tree Ψ_{50} hydraulic safety margin (Ψ_{50} - Ψ_{min}) and normalized non-structural carbohydrates (NSC) at, or prior to, mortality from drought for angiosperm (A, blue circles) and gymnosperm (N, red triangles) species. NSC data shown are means for aboveground woody tissue (bole, branch, stem, or twig), normalized as a percent of surviving or control trees in each case. Linear regressions were fitted separately for angiosperm and gymnosperm trees, and the significant relationship is shown for gymnosperm data. However, the linear regression in gymnosperm species was dependent upon inclusion of the outlier, *Callitris rhomboidea* (upper right of B); without this case the relationship was not significant ($p > 0.05$, linear regression).


A) Non-tropical Angiosperms
Deciduous
Evergreen
NSC (% change)
300
200
100
0
-100
P. balsamifera [2]
P. tremuloides [2]
E. globulus [4]
E. radiata [5]
E. radiata (+4°C) [5]
E. smithii [4]
B) Tropical Angiosperms
NSC (% change)
D. lanceolata [7]
D. oxleyanus [7]
H. nervosa [7]
K. excelsa [7]
P. malaanonan [7]
P. tormentella [7]
S. argentifolia [7]
S. beccariana [7]
S. marophylla [7]
S. parvifolia [7]
C) Gymnosperms
Leaf
Root
Bole, Branch, Stem, Twig
NSC (% change)
High CO2
Low CO2
High CO2
Low CO2
C. rhomboidea [8]
C. rhomboidea [8]
J. osteosperma [9]
P. abies [10]
P. abies [11]
P. abies [11]
P. edulis [9]
P. edulis [12]
P. edulis [13]
P. edulis [14]
P. flexilis [19]
P. radiata [4]
P. radiata [8]
P. radiata [8]
P. sylvestris [15]
S. sempervirens [18]

Supplementary Figure 6. Relative change in non-structural carbohydrates (NSC) over time during experimental drought between initial or pretreatment and at-mortality assessments from studies where such data were available. The normalization used in this figure is the percent change in NSC from initial observations or start of the experiment to mortality for drought treatment trees, an alternative normalization to that used in Figure 1 which was based on mortality–control tree differences. Data are shown for non-tropical (A) and tropical angiosperm (B) and gymnosperm conifer (C) species, and for each tissue analyzed in each study. In all panels for cases where individual data were available, boxes indicate the 25% and 75% quartiles, whiskers indicate the extent of data, and black bars indicate the mean. For cases where only means and a measure of variability were available, means are indicated with squares and error bars are one standard error. Significant differences in NSC concentration between drought trees at mortality and at the start of each experiment for each tissue of each species are indicated with an asterisk ($p < 0.05$, ANOVA). For starch values in case 15 (panel C), values in parentheses indicate maximum values for two tissues which are beyond the extent of the y-axis scale. The symbol "M" indicates data from a study on mature trees; all other data are from studies of seedlings, saplings, and small trees (Supplementary Table 1). Sample size for all data analyzed for Supplementary Figure 6 are available in Supplementary Table 5. A comparison of mean results between the normalization used in Figure 1 and this figure is available in Supplementary Table 7.