

CAUSES, CONSEQUENCES, AND THE FUTURE OF FOREST MORTALITY DUE TO CLIMATE CHANGE

KLIMATSKE SPREMEMBE IN MORTALITETA DREVES V GOZDNIH EKOSISTEMIH – VZROKI, POSLEDICE IN PRIČAKOVANJA

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ABSTRACT

Mortality of forest trees is growing at an accelerating rate due in part to increasing severity and frequency of droughts. The consequences of increasing forest mortality range from impacts on timber and tourism revenue, reductions in fuelwood availability and carbon storage, and feedbacks that accelerate climate changes. Unfortunately, our understanding of where, when, and how forests die is extremely limited, precluding us from forecasting future changes in forest composition and services. Here we review the state of current knowledge regarding mortality processes, and highlight the urgent scientific challenges that must be overcome if we are to adequately plan for future changes in forest survival and mortality. We suggest that forest monitoring through inventory networks and newly emerging remote sensing techniques should be a high priority for maintenance and development, because only through these observations can we determine what regions and species are most vulnerable to climate change. These datasets are also critical for evaluation of regional to global models of forest dynamics. Without accurate models, forecasts of future forest composition cannot be considered reliable. Furthermore, experimental tests of how the dominant global forest species die are needed to enable models to simulate mortality correctly. Lastly, experimental tests of forest management strategies that can alleviate stress under the novel climate regimes the globe is now experiencing are essential to allow planning for mitigation options in the forestry sector. Increasing forest mortality is now inevitable given the global energy portfolio; however, the ability of science and forestry to quantify, understand, predict, and mitigate impacts on forests remains a viable option to allow planning for future forest management to minimize impacts on the Earth's forests.

Key words: carbon sink, tree mortality, forest management, adaptation and mitigation

IZVLEČEK

Mortaliteta dreves v različnih delih sveta se v zadnjem času hitro povečuje predvsem zaradi povečevanja števila in trajanja suš. Posledice povečane mortalitete dreves so večplastne in se kažejo tako pri lesnoproizvodni funkciji kakor tudi pri različnih drugih funkcijah gozdov (od rekreacijske do hidrološke). Nenazadnje ima povečana mortaliteta dreves tudi ključen vpliv na ponor ogljika v gozdnem ekosistemu – ponor se spremeni v vir, to pa lahko ključno vpliva na povečevanje CO₂ v atmosferi in na segrevanje ozračja. V prispevku smo pripravili pregled stanja na področju raziskav procesov propadanja dreves, hkrati pa izpostavljamo pomen raziskav s tega področja, če se želimo v prihodnje ustrezno odzvati in ublažiti posledice klimatskih sprememb na gozdne ekosisteme in znižati mortaliteto dreves (kot posledico klimatskih sprememb). Uvajanje metod daljinskega zaznavanja, podatke nacionalnih inventur in intenzivnega monitoringa gozdnih ekosistemov izpostavljamo kot ključne elemente, ki nam omogočajo spremljanje, prepoznavanje in vrednotenje procesov v gozdnih ekosistemih. Omogočajo nam tudi prostorsko lokacijo najbolj ogroženih drevesnih vrst in gozdnih ekosistemov. Podatkovne zbirke so ključne za evaluacijo regionalnih in globalnih modelov dinamike razvoja gozda, brez teh podatkov so namreč rezultati modelov nezanesljivi. Dodaten vir podatkov, ki jih uporabljamo za modeliranje mortalitete dreves, so specifične raziskave, s katerimi skušamo razumeti procese umiranja dreves, kaj ga pospešuje in kaj zavira. Naraščajoča mortaliteta gozdnih ekosistemov je globalni fenomen, ki ga lahko s pomočjo novih spoznanj ovrednotimo, razumemo, predvidimo in z ustreznimi ukrepi tudi ublažimo. Pri tem poudarjamo ključno vlogo temeljnih in aplikativnih raziskav, dolgoročnih zbirk podatkov in novih, prilagojenih, gozdnogojitvenih in gozdnonačrtovalskih ukrepov, s katerimi bi lahko zmanjšali mortaliteto gozdov in jih naredili bolj odporne proti zaostrenim okoljskim razmeram.

Ključne besede: ponor ogljika, mortaliteta dreves, gospodarjenje z gozdom, prilagajanje in blaženje posledic klimatskih sprememb

GDK 56:111.83:422.22(045)=111

Prispelo / Received: 11. 11. 2013

Sprejeto / Accepted: 26. 11. 2013

1 INTRODUCTION

1 UVOD

Mortality of vegetation has been a focal issue for humans from before recorded history, due to its impact on fuelwood, shelter, and food availability (Anderegg et al. 2012a). In recent history, i.e. the last two centuries, drought-induced vegetation stress and mortality have frequently caused significant impacts on humans (e.g. crop losses, reduced timber production); however, climate extremes that caused these impacts typically recover to initial conditions, allowing ecosystem recovery and subsequent lessening of the impacts on the human populations that rely on ecosystem services. Global fossil fuel emissions to meet the growing human energy demand is chronically raising atmospheric greenhouse gas concentrations, however, which is already causing a globally unprecedented shift in climate to a new state of continual warming and more frequent and severe droughts (Allison et al. 2009). This chronic rise in drought conditions is resulting in significant losses of forest and crop production globally, with long-term consequences that are not yet understood, but are anticipated to have large negative consequences on both global ecology and human welfare.

Our objective in this paper is to review the state of the knowledge regarding climate change as it pertains to ecosystem survival. Every living thing eventually dies, but the focus here is the recent acceleration in the rate of forest and woodland mortality (Breshears et al. 2005, Allen et al. 2010). In particular, we will review our current understanding of current and future climate impacts on forests, and needed approaches to quantify, understand, and predict forest mortality. We will focus on drought because it is arguably the climate factor with the greatest current and forecasted impact on global forest mortality change over the next century (Allen et al. 2010). We will conclude with a review of the approaches to monitoring and understanding forest mortality that deserve the greatest emphasis in the upcoming years to allow improved anticipation, understanding, and mitigation of forest mortality in response to drought.

2 THE RISK OF ACCELERATING GLOBAL VEGETATION MORTALITY

2 GLOBALNA NEVARNOST POSPEŠENEGA PROPADANJA / MORTALITETE RASTLIN

Drought-associated mortality of woody plants and canopy dieback (loss of aboveground biomass while the belowground survives and regenerates) events have been documented throughout all six vegetated continents and are increasing in spatial and temporal frequency (Allen *et al.* 2010, McDowell et al. 2011). Accelerating rates of mortality have been observed as both regional-

scale die-offs (Breshears et al. 2005, Phillips et al. 2009) and as more insidious increases in background mortality (van Mantgem et al. 2009, Peng et al. 2011). Thus far, evidence suggests that no biome is immune from increasing mortality. Both widespread mortality events and chronic rises in mortality have been observed in wet systems such as the rainforests of southeast Asia and the Amazon (Phillips et al. 2011), cold systems such as the boreal forest (Beck et al. 2011, Peng et al. 2011), and temperate systems such as western North America (Breshears et al. 2005, Williams et al. 2013) and Europe (van Mantgem et al. 2009, Carnicer et al. 2011).

New evidence suggests the current acceleration of forest mortality will continue at even greater rates with warming surface temperatures (Galbraith et al. 2011, Williams et al. 2013, Jiang et al. 2013). This result is forecasted even if regional precipitation trends remain unchanged in the future because warming surface temperatures cause vegetation stress to be greater for any given precipitation than they were historically. Mortality will likely increase because rising temperature impacts plants in multiple negative ways. First, temperature rise induces higher rates of respiration, resulting in faster depletion of carbohydrate stores that are used for fueling growth, metabolism, and defence (Atkin et al. 2007, McDowell et al. 2008, Adams et al. 2009). Second, rising temperatures allow faster maturation of insect and pathogen species, allowing a greater number of generations and a larger climate window for attack on stressed plants (Raffa et al. 2008). Lastly, evaporative demand for water increases exponentially with temperature, thus rising surface temperature causes greater water loss from ecosystems and more rapid stomatal closure and hence elevated constraints on photosynthesis (McDowell et al. 2011). Thus, periods of low precipitation will have severer impacts on vegetation survival in the future than they have in the past (Williams et al. 2013). Given the current and predicted rates of surface warming (Allison et al. 2009), this impact is only likely to grow throughout the 21st century.

3 THE CONSEQUENCES OF VEGETATION MORTALITY

3 POSLEDICE PROPADANJA / MORTALITETE RASTLINSTVA

Mortality events drive rapid and large-scale shifts in ecosystem structure and function, causing significant and lasting impacts on hydrology, carbon sequestration, and regional economies (reviewed in McDowell et al. 2008, Adams et al. 2010, Anderegg et al. 2012). While each of these consequences can cause significant regional impacts, we focus here on the global climate

consequences of mortality. The impacts of current and future vegetation mortality on global climate has not been quantified, but both empirical and modelling results suggest it is a large potential climatic tipping point (Friedlingstein et al. 2006, Sitch et al. 2008, Allison et al. 2009, Jiang et al. 2013, Arora et al. 2013). This is particularly true for forests, which store over 50% of carbon sequestered terrestrially, contribute more to the terrestrial sink per area than any other land cover type, and assimilate an important portion of anthropogenic emissions (Bonan, 2008). However, distributed plot estimates suggest that mortality released 1.6 and 2.2 Pg C from the Amazon basin during the “100 year” droughts in 2005 and 2010, respectively, converting the basin from a carbon sink to source (Phillips et al. 2009, Lewis et al. 2011). Similar reversals of ecosystem carbon sinks to sources have been documented throughout temperate and boreal regions of North America using plot inventories, eddy covariance measurements, and models (Kurz et al. 2008, Amiro et al. 2010, Hicke et al. 2012).

Simulations by Dynamic Global Vegetation Models (DGVMs) consistently suggest forest mortality will release huge amounts of carbon into the atmosphere. Compa-

rison of static to dynamic DGVM runs have demonstrated that vegetation mortality (and slow recovery) may cause the global land surface to switch from its current status as a net carbon sink status to a net carbon source well before AD 2100 (Friedlingstein et al. 2006, Sitch et al. 2008, Arora et al. 2013). Using the Community Land Model (CLM(CN), v 3.5), it has been suggested that warming alone will cause >50% loss of evergreen needleleaf forests from western North America by 2100, resulting in a loss of > 6 GtC (equivalent to 6 years of USA fossil fuel emissions (Figure 1, Jiang et al. 2013). Jiang et al. (2013) further predict that all conifer forests will be gone from Southwestern USA by 2050. The prediction of nearly complete mortality of conifers in Southwestern USA was supported by an independent assessment that developed a strong predictive relationship between tree-ring growth, mortality, and climate, and then using the empirical model along with climate model ensemble predictions to forecast future growth and survival (Figure 1; Williams et al. 2013). Taken together, the overwhelming bulk of evidence points toward a rapidly declining carbon sink due to current and future increases in forest mortality. However, the strength of this decline is highly uncertain,

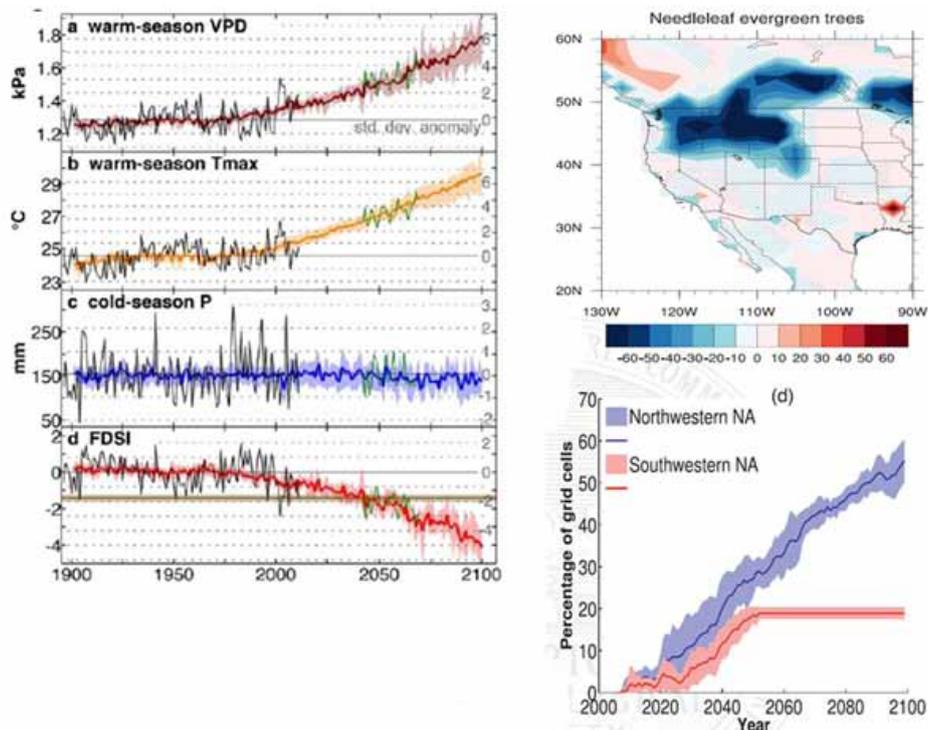


Fig 1: Forecasted drought stress and death based on empirical climate relationship (left, Williams et al. 2013) or based on CLM4CNDV process model (right, Jiang et al. 2013). The flattening out of the Southwest time series near 2050 indicates complete disappearance of the needleleaf trees. Interestingly, the timing of this disappearance of needleleaf trees corresponds with when FDSI (Forest Drought Stress Index) is expected to surpass megadrought conditions.

Slika 1: Pričakovani sušni stres in mortaliteta dreves na osnovi (a) empiričnih povezav s klimo (levo, William in sod. 2013) in (b) na osnovi modeliranja s procesnimi modeli CLM4CNDV (desno, Jiang in sod. 2013) za Severno Ameriko. Izravnava časovne vrste za JZ del severne Amerike od leta 2050 dalje pomeni popolno izginotje iglavcev v tem predelu. Leto 2050 se časovno ujema s trenutkom, ko naj bi indeks FDSI (ang.=Forest Drought Stress Index) presegel mejno vrednost za “supersušo”.

with model predictions of cumulative terrestrial CO₂ uptake varying up to 494 Pg C by 2100, equal to ~50 years of anthropogenic emissions (Sitch et al. 2008).

Widespread forest mortality also induces biophysical feedbacks on climate (Bonan 2008). For example, the massive mortality event in British Columbia, Canada, caused a sustained regional increase in surface temperature by ~1°C due to an increase in sensible heat flux from the Earth's surface to the atmosphere (Maness et al. 2012). Similarly, in the CLM(CN) simulations mentioned above (Jiang et al. 2013), the >50% loss of needleleaf evergreen forests caused a 20% reduction in evapotranspiration, increasing sensible heat flux, and exacerbation of surface temperature rise of ~4°C by 2100. These climate feedbacks are concerning because they indicate that forest mortality begets more forest mortality, with the cessation of mortality driven by exhaustion of live forests (Williams et al. 2013).

4 THE MECHANISMS OF DROUGHT-INDUCED MORTALITY

4 FIZIOLOŠKI MEHANIZMI S SUŠO POVZROČNE MORTALITETE

Despite centuries of interest and a large increase in the study of forest mortality over the last decade, little is known about the exact mechanisms by which trees die (Sala et al. 2010). Most people understand that droughts kill trees, yet no one can predict why some trees die, while others survive during drought. This paucity of knowledge is a result of a lack of empirical experimentation (McDowell and Sevanto 2010). Beyond fundamental understanding, this lack of understanding has created a significant limitation on our ability to model future forest mortality (McDowell et al. 2011).

Theoretical analysis of plant mortality mechanisms nearly always suggests that it results from a complex interaction of plant water and carbon balance with community dynamics of biotic pests, such as insects, bacteria, and fungi, and their predators (Manion et al. 1981, Waring et al. 1987, Martinez-Vilalta et al. 2002, McDowell et al. 2008, McDowell et al. 2011). In an attempt to provide a testable framework, McDowell et al. (2008) proposed two mutually inclusive mechanisms of mortality. Hydraulic failure, defined as the process of dehydration and subsequent metabolic failure, is proposed to occur through prolonged loss of water that is not replaced. Carbon starvation, defined as the process of depletion of carbohydrate reserves that results in failure to maintain metabolism or defensive capability, results from stomatal closure to avoid dehydration, which has the subsequent effect of constraining photosynthesis while respiratory metabolism continues (McDowell 2011). These

processes have feedbacks, by which a decline in carbohydrate supply may cause increasing hydraulic failure, and vice versa (McDowell 2011, McDowell et al. 2011). Furthermore, these processes are hypothesized to interact with biotic agents, by which acceleration of the hydraulic failure and carbon starvation processes allow greater rates of biotic attack, greater reproduction of biotic populations, and subsequently greater rates of biotically enhanced hydraulic failure and carbon starvation (McDowell et al. 2008, 2011). However, much of these ideas is based on fundamental physiological theory and indirect evidence of the literature, thus the mechanisms of mortality remain in question (Sala et al. 2010).

Newly emerging experimental evidence confirms that the hydraulic framework appears correct. The processes of hydraulic failure and carbon starvation are nearly always observed to co-occur in both observational studies and during experimental drought-manipulations that induce mortality (Galiano et al. 2011, Galvez et al. 2011, 2012, Levanič et al. 2011, Anderegg et al. 2012b, Plaut et al. 2012, Quirk et al. 2013, Sevanto et al. 2013, Hartmann et al. 2013). However, the relative dominance of hydraulic failure versus carbon starvation in driving mortality appears to depend on the rate of stress onset in plants, with faster drought causing more hydraulic failure and vice versa (Mitchell et al. 2013; consistent with the predictions of McDowell et al. 2008). Despite these consistent results, there remains a large amount of variation in the degree of hydraulic failure and carbon starvation observed prior to mortality that is currently un-explained.

5 FUTURE RESEARCH

5 BODOČE RAZISKAVE

There are numerous questions that remain to be answered regarding the mechanisms of mortality. Amongst the most important is to determine what level of understanding is truly required to allow accurate modelling of future forest survival and mortality. Understanding the exact processes of mortality is often touted as essential to allow models to correctly capture non-linear properties of physiological-climate relationships that may emerge in the future (e.g. McDowell et al. 2011); however, given the lack of testing of models thus far, we do not know if this hypothesis is accurate. From a fundamental biological perspective, clever manipulative studies are needed to understand the exact cascade of processes during death, such as has been done through shading (Marshall and Waring 1985, Sevanto et al. 2013) and CO₂ manipulation (Quirk et al. 2013) and with the use of molecular tools to unravel cause and effect (e.g. Stitt and Zeeman 2012). This type of studies must be done on a range of plant types, including gymnosperms and

angiosperms from a range of biomes and tree life-stages (e.g. seedling to mature), in order to understand the variation in mortality mechanisms that exist.

We currently have no global monitoring system of vegetation mortality, which has numerous consequences on our understanding and prediction because we do not know which biomes or vegetation types are most vulnerable, we do not understand the environmental drivers of mortality, and we have no datasets to use for model evaluation (Allen et al. 2010). Forest inventory networks provide potential regional scale assessment of mortality in select countries (e.g. Carnicer et al. 2011, Williams et al. 2013), but the long term solution to this data gap is likely to arrive via satellite-remote sensing (Coops et al. 2006, Mu et al. 2013). However, methods to process the exorbitantly large global datasets of intermediate scale spatial resolution imagery, e.g. 30m² via Landsat, must first be resolved before such technology can be applied at large scales.

Land management practices that maximize the likelihood of tree survival are also critical to investigate if we are to mitigate and adapt forest production for the future. Practices such as forest thinning may be very effective in some regions to reduce drought-stress by increasing water, nutrient, and light availability (McDowell et al. 2006). Planting drought-tolerant genotypes of forest species in locations previously thought too wet for them is another strategy that should be investigated to maximize future forest survival. Lastly, in areas of particularly massive mortality (e.g. Breshears et al. 2005); conservation of refugia where the climate or edaphic properties may prolong survival of important species, should be a high priority.

6 ACKNOWLEDGMENTS

6 ZAHVALA

We appreciate the support of DOE-BER, LANL-LDRD, and EUFORINNO project (FP7-REGPOT-2012-21013 #315982).

7 REFERENCES

7 VIRI

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E. 2009a. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences* 106(17): 7063-7066.
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennerier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660-684.
- Allison I, Bindoff NL, Bindschadler RA, Cox PM, de Noblet N, England MH, Francis JE, Cruber N, Haywood AM, Karoly DJ et al. 2009. The Copenhagen diagnosis 2009: Updating the world on the latest climate science, The University of New South Wales Climate Change Research Centre.
- Amiro, B. D., et al. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res.* 115: G00K02, doi:10.1029/2010JG001390.
- Anderegg, W.R.L., J. M. Kane, L.D.L. Anderegg. 2012a. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* DOI:10.1038/NCLIMATE 1635.
- Anderegg, W.R.L, Callaway E. 2012b. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology* doi: http://dx.doi.org/10.1104/pp.112.
- Arora V, et al. 2013. Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models. *J. Climate*. doi:10.1175/JCLI-D-12-00494.1, in press.
- Atkin, O.K., Scheurwater, I. and Pons, T.L. (2007). Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures *New Phytologist* 174: 367-380.
- Beck, P.S.A., G. P. Juday, C. Alix, V.A. Barber, S.E. Winslow, E.E. Sousa, P. Heiser, J.D. Herriges, S.J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters* 14, 373-379.
- Bonan, G.B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320(5882): 1444-1449.
- Boone C.K. et al. 2011 Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Can. J. For. Res.* 41: 1174-1188.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, F.W. 2005. Regional vegetation die-off in response to global-change type drought. *Proceedings of the National Academy of Science*. 102: 15144-15148.
- Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sanchez, J. Penuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Science*. 108, 1474-1478.
- Chambers et al. 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *PNAS* 110(10): 3949-3954.
- Coops, N. C., Johnson, M., Wuler, M. A., & White, J. C. 2006. Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. *Remote Sensing of Environment* 103: 67-80.
- Friedlingstein P., et al. 2006. Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *Journal of Climate* 19: 3337-3353.
- Frolking S, et al. 2009. Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J. Geophysical Research*, /10.1029/2008JG000911.
- Galbraith D, et al. 2011. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytologist* 187: 647-665
- Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytologist*, 190, 750-759. Galvez, D.A., Landhäusser, S.M. & Tyree, M.T. (2011) Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiology*, 31, 250-257.

- Galvez, D.A., Landhäusser, S.M. & Tyree, M.T. (2013) Low root reserve accumulation during drought may lead to winter mortality in polar seedlings. *New Phytologist*, n/a-n/a.
- Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist*. doi:10.1111/nph.12174
- Hartmann, H., Ziegler, W. & Trumbore, S. (2013) Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Functional Ecology*, in press.
- Hicke JA, Allen CS, Desai AR, Dietze MC, Hall RJ, Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN et al. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* 18: 7-34.
- Jiang, X., S. Raucher, T.D. Ringler, D. Lawrence, P. Williams, M. Cai, N.G. McDowell. 2013. Increasing risk of tree mortality in western North America towards the end of the 21st century. *Journal of Geophysical Research*, 10.1174/JCLI-D-12-00430.1
- Kennedy, R.E., Yang, Z., Cohen, W.B., Pfaff, E., Braaten, J., & Nelson, P. 2012. Spatial and temporal patterns of forest disturbance and regrowth within the area of the Northwest Forest Plan. *Remote Sensing of Environment* 122, 117-133.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L. Ebata, T., Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* DOI: 10.1038/nature06777.
- Levanič, T., M. Čater, and N.G. McDowell. 2011. Associations between carbon isotope discrimination, growth rate and mortality in a *Quercus robur* forest. *Tree Physiology* doi: 10.1093/treephys/tpq111
- Limousin JM, Bickford CP, Dickman LT, Pangle RE, Hudson PJ, Boutz AL, Gehres N, Osuna JL, Pockman WT, McDowell NG. 2013. Regulation and acclimation of leaf gas-exchange in a piñon-juniper woodland exposed to three different precipitation regimes. *Plant, Cell & Environment*, in press.
- Lewis SL, Brando PM, Phillips OL, van der Heijden GM, Nepstad D. 2011. The 2010 Amazon drought. *Science* 331: 554.
- Luo Y, Randerson J, Abramowitz G, Bacour GC, Blyth EM, Carvalhais N, Ciais P, Dalmonech D, Fisher JB, Fisher RA et al. 2012. A framework of benchmarking land models. *Biogeosciences* 9: 3857-3874.
- Maness H, PJ Kushner, I Fung. 2012. Summertime climate response to mountain pine beetle disturbance in British Columbia. *Nature Geoscience* 6, 65-70
- Manion, P.D. 1981. *Tree Disease Concepts*. Upper Saddle River, NJ, USA: Prentice Hall.
- Marshall, J.D., Waring, R.H. 1985. Predicting fine root production and turnover by monitoring root starch and soil temperature. *Canadian Journal of Forest Research* 15: 791-800.
- Martínez-Vilalta, J, Piñol J, Beven K (2002) A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecological Modelling*, 155, 127-147.
- McDowell, N.G., Pockman, W., Allen, C., Breshears, D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D., Yepez, E. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb? *New Phytologist* 178: 719-739.
- McDowell NG, Sevanto S. 2010. The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytologist* 186: 264-266.
- McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155: 1051-1059.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* 26: 523-532.
- Moorcroft PR. 2006. How close are we to a predictive science of the biosphere? *Trends in Ecology and Evolution* 21: 400-407.
- Mitchell PJ, O'Grady AP, Tissue DT, White DA, Ottenschlaeger ML, Pinkard EA (2013) Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality, *New Phytologist*, vol.197, no.3, pp 862-872
- Mu, Q, Zhao M, Kimball J, McDowell N, Running S. 2013. A remote sensed global terrestrial drought severity index. *Bulletin of the American Meteorological Society* 94: 83-98.
- Peng S, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forest. *Nature Climate Change* 1: 467-471.
- Phillips OL, et al., 2009. Drought sensitivity of the Amazon forest. *Science* 323: 1344-1347
- Phillips OL, et al. 2011. Drought-mortality relationships for tropical forests. *New Phytologist* 187: 631-646
- Plaut JA, Yepez EA, Hill J, Pangle R, Sperry JS, Pockman WT, McDowell NG. 2012. Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought. *Plant, Cell and Environment* 35: 1601-1617.
- Quirk J, McDowell NG, Leake JR, Hudson PJ, Beerling DJ. 2013. Carbon dioxide starvation, drought, and Cenozoic forest retreat. *American Journal of Botany* 100(3): 582-591.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* 58(6): 501-517.
- Randerson JT. 2013. Climate science: global warming and tropical carbon. *Nature* 494, 319-320
- Ryan MG. Effects of climate change on plant respiration. 1991. *Ecological Applications* 1:157-167.
- Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186: 274-281.
- Seidl et al. 2011. Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling* 222(4): 903-924.
- Sevanto S., N.G. McDowell, L.T. Dickman, R. Pangle, and W.T. Pockman. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell and Environment* in press.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology* 14: 1-25.
- Skurikhin, A., S. Garrity, N.G. McDowell, D.M. Cai. 2013. Automated tree crown detection and size estimation using multi-scale analysis of high resolution satellite imagery. *Remote Sensing Letters*, 4:465-474.
- Stitt, M. and S.C. Zeeman. 2012. Starch turnover: pathways, regulation and role in growth. *Current Opinion in Plant Biology* 15, 282-292.
- Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harman, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323: 521-524.
- Waring, R.H. 1987. Characteristics of trees predisposed to die. *Bioscience* 37: 569-577.
- Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3: 292-297.