INTRODUCTION

1.) Atmospheric CO2 is rising (IPCC 2013).

This has consequences for woody plant physiology and growth – the “CO2 fertilisation effect” http://link.springer.com/chapter/10.1007/978-1-4615-2816-6\_3

Physiological responses (of C3 plants) include:

* Stimulation of CO2 assimilation and photosynthetic rate (Gunderson & Wullschleger, 1994)
* Reduced stomatal conductance (Ainsworth & Rogers, 2007)
* FX are Variable between experiments “The effects of elevated Ca on both A and gs vary among experiments with forest trees (e.g. Eamus & Jarvis, [1989](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0013); Curtis & Wang, [1998](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0007); Medlynet al., [1999](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0035), [2001](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0036); Ainsworth & Long, [2005](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0001); Warren et al., [2011](http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02526.x/full#gcb2526-bib-0056)). “ - (Barton et al., 2012)
* Increased WUE (Holtum & Winter, 2010; Keenan et al., 2013; van der Sleen et al., 2014)
* Growth responses:
* Depend on availability of water and nutrients (Körner, 2006; Manea & Leishman, 2014; Reich et al., 2006) OR BOTH (Reich, Hobbie, & Lee, 2014).
* Biomass allocation (aboveground / belowground) (RMF affected by eCO2 under dry conditions, but not by much under normal conditions. Sp. response was highly variable.) (X. Wang & Taub, 2010). Another meta-analysis found increased root biomass and increased RMF under eCO2.
* Fine root production and turnover stimulated under eCO2 (Lipson, Kuske, Gallegos-Graves, & Oechel, 2014; Matamala & Schlesinger, 2000; K. S. Pregitzer et al., 1995; K. Pregitzer et al., 2000).
* Tissue densities and associated position along economic spectra (do these even hold under eCO2?) (Reich, 2014).
  + SLA is reduced at eCO2 (D. Wang, Heckathorn, Wang, & Philpott, 2012)
  + “Although a meta-analysis is lacking, accumulation of nonstructural carbohydrates is likely to be the main factor for the decrease in SLA ([Wong, 1990](http://onlinelibrary.wiley.com/doi/10.1046/j.1469-8137.2003.00680.x/full#b59); [Roumet*et al*., 1996](http://onlinelibrary.wiley.com/doi/10.1046/j.1469-8137.2003.00680.x/full#b27)) resulting in an increase in leaf density ([Roumet *et al*., 1999](http://onlinelibrary.wiley.com/doi/10.1046/j.1469-8137.2003.00680.x/full#b64))." (Poorter & Navas, 2003). Also (Bader, Siegwolf, & Körner, 2010).
  + Root tissue density suggested to increase under eCO2 (Eissenstat, Wells, & Yanai, 2000) but this has not been demonstrated in the field (Iversen, Ledford, & Norby, 2008) “Suberization of roots increases with age and during stress (drought, high salinity, nutrient deprivation, anoxia, etc.)” (Steudle, 2000)
  + Stem density??

2.) Riparian plants experience frequent waterlogging and inundation. Waterlogging is distinct from complete inundation, affects only the root zone (Webb, Wallis, & Stewardson, 2012). Riparian plants may experience cycles of waterlogging and drying for their entire life cycle. Woody species often colonise bars and benches that are raised above the main channel, so root zone waterlogging may be more s common stress than actual inundation.

For many plants waterlogging can be highly stressful.

* Anoxia in the root zone is associated with production reactive oxygen species, and of toxic ions by microbes are the most significant stressors (Colmer & Voesenek, 2009; Voesenek & Bailey-Serres, 2015) “electrochemical soil changes resulting in higher concentrations of toxic elements including manganese (Mn2+), iron (Fe2+) and sulfide (H2S, HS?,S2?) (Bailey-Serres & Voesenek, 2008; Lamers et al., 2012; Zeng et al., 2012)”. “ROS are produced at the onset of flooding-induced O2 deprivation as a consequence of the inhibition of mitochondrial electron transport and generation of superoxide that is converted to hydrogen peroxide by dismutation (Santosa et al., 2007). Increases in superoxide and hydrogen peroxide are prevalent upon reaeration (Blokhina&Fagerstedt, 2010; Steffens et al., 2013; Fig. 3).” ( Voesenek 2015)
* Maintaining roots in anoxic conditions bears a high metabolic cost (Colmer & Voesenek, 2009; Drew, 1997), esp. when metabolism shifts to anaerobic pathways.
* Root function is weakened due to reduced respiration; water and nutrient uptake is impaired (Piedade, Ferreira, Wittmann, Buckeridge, & Parolin, 2010; Voesenek & Bailey-Serres, 2015). Root mortality may occur.
* Stomatal closure may occur reducing ability to assimilate carbon. Stomatal closure may be due to loss of function of root signalling (Else, Janowiak, Atkinson, & Jackson, 2009)

Waterlogging induces a range of physiological and morphological responses in plants, resulting in different growth responses. Stress is ultimately determined by the degree to which plants are adapted to waterlogged soil conditions (T. T. Kozlowski, 1984; Voesenek & Bailey-Serres, 2015).

* Aerenchyma and adventitious roots are common morphological adaptations (Colmer & Voesenek, 2009; Evans, 2004)
* Various physiological strategies also exist (see Voesenek)
* Waterlogging of flood tolerant plants may not necessarily decrease plant growth (Megonigal, Vann, & Wolf, 2005; Webb et al., 2012).
* “Additionally, in legumes that fix atmospheric N2 gas by Rhizobium in nodules. The formation of nodules and its activity, which has an important role for nitrogen supply and growth for legumes, can be damaged by waterlogging (Linkemer et al., 1998)” – Shimono (can’t get reference)

3.) Very little literature describes the interactive effects of elevated atmospheric CO2 and waterlogging or flooding on plant growth.

- Megonigal 2005 (baldcypress and aquatic plant)

- found that CO2 stimulation of PS wasn’t reduced by flooding but biomass was only increased in control plants. eCO2 increased aquatic plant biomass irrespective of flooding. They actually flooded their plants though, and their non-flooded treatment (-10cm water table) was in fact equivalent to our waterlogged treatment. (glasshouse)

- Arenque 2014 (Amazonian Senna sp.)

- Opposite response compared with *T. distichum* in Megonigal et al. study. eCO2/waterlogged Senna reticulata (Amazonian highly flood tolerant leguminous tree) showed greater increment in biomass compared with aCO2/waterlogged (open top chambers).

- Shimono et al. 2012

- found no evidence for a waterlogging / CO2 interaction on plant growth or stomatal conductance. But say at the end of their discussion that their results ‘partially suggest’ that eCO2 may alleviate waterlogging stress.

Interaction between CO2 and waterlogging / flooding appears to be variable.

Various hypotheses have been put forward with respect to the potential effect of eCO2 on waterlogged plants:

* Alleviation of anoxic drought via increased water use efficiency
  + “However, elevated [CO2] might alleviate the damage caused by waterlogging by waterlogging by preventing dehydration (Kramer and Jackson, 1954; Bradford and Hsiao, 1982; Grassini et al., 2007), and by increasing photosynthesis that supplies carbohydrates to roots, allowing more efficient production of adenosine triphosphate (ATP).”

Why is looking at recovery from waterlogging important? Recovery following stress events may be more important to fitness than tolerance of the stress (Gutschick & BassiriRad, 2003). ROX generation following reaeration is likely to be a significant stress (Drew, 1997). No studies have looked at the influence of eCO2 on recovery following waterlogging.

4.) The objective of this study was to investigate interactive effects between eCO2 and waterlogging on gas exchange, growth, biomass allocation and positioning along economic spectra.

We asked:

* Are eCO2 effects on gas exchange altered by waterlogging, and is this response maintained following recovery from waterlogging?
* Is stimulation of biomass production by eCO2 diminished following recovery from waterlogging?
* Does CO2 mediate biomass allocation or functional traits in response to waterlogging, or following recovery from waterlogging?

We hypothesised:

* That eCO2 stimulation of photosynthesis would be maintained during waterlogging and following a refractory period
* The eCO2 effect on biomass production and allocation would be maintained following recovery from waterlogging
* eCO2 interaction with waterlogging would be evident for root traits but not aboveground traits