Woody thickening: a consequence of changes in fluxes of carbon and water on a warming globe?

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Abstract

Understanding patterns, rates and controls of water and CO_2 exchange between land surfaces and the atmosphere is central to the sciences of meteorology, ecology, hydrology, ecophysiology, forestry and related endeavours. Measurements involving sapflow sensors, eddy covariance and remote sensing have contributed substantially to our understanding of these issues. In this talk, we apply a combination of methods in order to apply a soil-plant-atmosphere model to the question: what is causing the globally observed phenomenon of woody thickening?

The density of woody plants in arid and semi-arid regions is increasing regionally and globally (Fensham et al., 2005, Hoffman et al., 1999, Bowman et al. 2001, Burrows et al. 2002). This can be deduced from analyses of tree-ring widths, forest inventory data, aerial photo-interpretation and from long-term monitoring sites (Spiecker et al., 2003). Potential causes of woody thickening have been extensively discussed in the past. Mechanisms that have been proposed include the (a) Walther model, which invokes competition for water and nutrients among the deeper roots of woody plants *versus* the shallower roots of shrubs and grasses; (b) a role for changes in the timing, intensity and frequency of fire; and (c) changes in herbivory by large herbivores. Such thickening may have a large impact on regional CO_2 budgets, atmospheric CO_2 concentration and ecosystem function and regional water budgets.

We propose an alternative mechanism to explain woody thickening based upon changes in water and carbon fluxes within the soil-plant-atmosphere continuum resulting from a change in global atmospheric conditions. Such a mechanism is global in reach, appears consistent with a number of phenomena and has several testable predictions, which we briefly discuss.

In this talk we present:

(a) the bio-physical conceptual basis of the model;
(b) supporting evidence from evapo-transpiration rates, run-off, soil moisture and changing atmospheric conditions associated with a warming global environment;
(c) results of a modelling analyses using the SPA model of Williams et al. (2001) as applied to an Australian open woodland.

The conceptual framework

The following observations constitute the *a priori* foundations for the model:

1. The concentration of CO_2 in the atmosphere ($[CO_2]_a$) has been increasing since the start of the industrial revolution.

2. This rise in $[CO_2]_a$ has two effects: (i) it increases rates of photosynthesis of woody plants, typically of about 30 to 50 %. Photosynthesis is enhanced more in woody shrubs (+45 %) than grasses (+38 %) or trees (+25 %) in response to CO_2 enrichment; and (ii) stomatal conductance of woody plants is

decreased by about 20 %. C4 grasses show a smaller response to CO_2 enrichment than C3 plants such as shrubs and trees.

3. The growth rate of trees and shrubs is enhanced by increased $[CO_2]_a$ because of the stimulation of photosynthesis and decreased photorespiration. Importantly, the proportional increase in tree growth is larger under xeric than mesic conditions.

4. Pan evaporation rates have declined globally, including across Australia.

We propose that these observations may explain the phenomenon of woody thickening. It is useful to note that there are three key predictions from this conceptual model. First, long-term trends in tree water-use-efficiency should be increasing; second, run-off should increase where woody thickening is occurring; finally enriched CO_2 studies should reveal an enhanced plant water status. These three predictions are discussed later.

Supporting evidence

1) A decrease in pan evaporation rates has been recorded for the northern hemisphere, Australia and New Zealand (Roderick and Farquhar, 2002, Roderick and Farquhar, 2004). In water-limited ecosystems, decreasing pan evaporation rates can best be explained by decreased wind speed and decreased solar radiation receipt at ground level (global dimming) because of increased cloud cover and atmospheric aerosol content. Vapour pressure deficit has decreased for water-limiting ecosystems of Africa, Australia and the Indian sub-continent (Nemani et al., 2003); this is another measure of a decreasing pan evaporation rate.

2) Because of a decrease in evaporative demand for water either soil moisture content must increase in the short-term or excess moisture must be lost through increased run-off and in the longer-term by increased water use by vegetation.

3) The prediction that increased run-off as a consequence of climate change is supported from both observational and simulation studies (Labat et al., 2004; Probst and Tardy, 1987). The high $[CO_2]_a$, of recent decades, compared to the levels observed in the 18th century, has also been recently invoked to explain this increased run-off (Gedney et al., 2006) through the observed response of stomatal conductance to $[CO_2]_a$, (Eamus and Ceulemans 2001; Medlyn et al. 2001).

4) There is evidence of global soil moisture increasing with positive soil moisture trends observed during the 20th century in the Ukraine, Mongolia and the western USA, for example (Robock et al., 2000; Robock et al., 2005, Hamlet et al. 2007, Hirabayashi et al. 2005). While models of global warming predict summer soil desiccation, there is no evidence for this even in regions that have been warming over the past 50 years. For arid and semi-arid regions of the southern hemisphere, however, evidence of increases in soil moisture is limited. Elevated moisture levels across land-use gradients have been documented in sparsely grassed, deep sand-dunes of the southern Kalahari. This higher soil moisture status has promoted the success of C3 shrubs and trees, including *Acacia mellifera* and *Rhigozum trichotomum.*

5) A second prediction from our model is that a reduced stomatal conductance in response to CO_2 enrichment and a concomitant enhancing of soil moisture stores (for at least some months of the year), will result in a more positive plant water status. There is ample evidence that an improved water status is observed under CO_2 enriched conditions (Eamus et al. 1995). Wullschleger et al. (2002) reviews many of the studies published between 1990 and 2000 and shows that improved water status is frequently observed in studies of CO_2 enriched environments. These differences were larger during drought than wetter conditions, as expected.

Testing the conceptual model

In order to test the conceptual model presented here, we ran the SPA model under a range of scenarios, which include different levels of atmospheric CO_2 concentration, rainfall, VPD and temperature, either in isolation (ie one factor at a time) or in combination. The SPA model is a detailed process based mechanistic model that has been successfully tested and validated across a range of diverse ecosystems, including Arctic tundra (Williams *et al*. 2000), Brazilian tropical rainforests (Williams *et al*. 1998, Fisher *et al*. 2006) and temperate Ponderosa pine forests (Williams *et al*. 2001). The SPA model predicts, amongst other parameters, carbon and water fluxes, leaf water relations and changes in soil moisture and is previously untested in Australian ecosystems.

We have recently successfully applied the SPA to a temperate open woodland in NSW.

Key results of the climate scenarios we applied to the open woodland can be summarised thus:

I. When CO_2 concentration was reduced to 80 % of ambient, stomatal conductance (g_s) and annual tree sapflow increased but GPP decreased. When CO_2 levels were increased above ambient, g_s and annual tree sapflow declined by between 10 and 60 % and leaf water potential was increased; most importantly GPP increased by almost 50 % when CO_2 levels were increased above ambient.
II. As annual rainfall ranged between 50 % and 150 % of current levels for this site (about 680 mm per y), g_s was unaffected. When rainfall was reduced to 50 % of current levels, but annual tree sapflow decreased by 20 %. When rainfall was increased by 50 %, annual sap flow was increased by 25 % and leaf water potential was increased. GPP increased by about 15 % for an increase in rainfall of 50 %.
III. As VPD was varied between - 25 % (wetter air) and + 25 % (drier air), g_s was unaffected. Annual tree sapflow was reduced when atmospheric water content increased (VPD declined) but increased by 20 % when atmospheric water content declined by 25 %. Simultaneously, leaf water potential declined. GPP decreased by about 15 % (ie GPP declined as the air became drier). This was attributed to a decline in leaf water potential and the impact that this had on C uptake on dry days.
IV. There was minimal response in any variable to a temperature increase of between 1 and 4 ^{o}C.
V. When atmospheric CO_2 concentration was increased to 550 µmol mol^{-1} in combination with decreased VPD (wetter air) of 25 % and temperature increased by 2 ^{o}C, g_s showed a minor decline but annual tree sapflow increased by 5 % and leaf water potential increased. Most importantly, GPP increased by 25%.

Conclusion

Clearly, we have a simple yet powerful explanation for the trend of increasing woody thickening observed in arid and semi–arid regions over the past 50-100 years. As pan evaporation rates have declined, the availability of soil moisture has increased (as evidenced by increased water potentials), effectively equivalent to increased rainfall. Simultaneously there is a decrease in stomatal conductance resulting from increased atmospheric $[CO_2]_a$ levels which were shown also to reduce tree sapflux. This has all resulted in an increased ecosystem-scale GPP which is translated into woody thickening. A final prediction from our conceptual model is that water-efficiency should have been increasing in woody plants for the past century because of the increase in photosynthesis and the decline in stomatal conductance arising from increased $[CO_2]_a$. In support of this prediction is the observation that GPP was increased and tree water use decreased in our final simulation. It is pertinent to note that long-term increase in WUE of trees that has been reported over the past 100 years using stable isotope analyses of tree rings (Hietz et al., 2005).

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