Hindawi Publishing Corporation
Research Letters in Ecology
Volume 2007, Article ID 37364, 5 pages
doi:10.1155/2007/37364

Research Letter

Is Climate Change a Possible Explanation for Woody Thickening in Arid and Semi-Arid Regions?

Derek Eamus and Anthony R. Palmer

Institute for Water and Environmental Resource Management, University of Technology Sydney, P.O. Box 123, 15 Broadway, NSW 2007, Australia

Correspondence should be addressed to Derek Eamus, derek.eamus@uts.edu.au

Received 4 October 2007; Accepted 9 December 2007

Recommended by Jianguo (Jingle) Wu

Increased woody plant density (woody encroachment or woody thickening) is a globally observed phenomenon. Similarly, increased atmospheric carbon dioxide concentrations and decreased pan evaporation rates are globally observed phenomena. In this paper, we propose that the former (increased woody plant density) is a product of the latter. We propose that decreased stomatal conductance and increased rates of carbon fixation arising from an enriched atmospheric carbon dioxide concentration, in conjunction with reduced rates of pan evaporation, result in increased woody plant density. We suggest that this is analogous to the increased woody plant density that is observed along rainfall gradients that span arid to mesic environments. From this conceptual model, we make three predictions, namely, that (a) long-term trends in tree water-use-efficiency should reveal increased values; (b) run-off data should show an increase where woody thickening is occurring; (c) enriched CO_2 experiments should reveal an enhanced plant water status. These three predictions are discussed and shown to be supported by experimental data.

1. INTRODUCTION

The density of woody plants in arid and semiarid regions is increasing regionally and globally [1–3]. Furthermore, increased forest growth has been observed in tree-ring analyses [4], forest inventory data [5], aerial photo-interpretation, and from long-term monitoring sites [3, 6, 7].

Potential causes of woody thickening have been extensively discussed [8, 9]. The Walther model invokes competition for water and nutrients [10–12] where the deeper roots of woody plants access deep stores of water. Alternatively, changes in the timing, intensity, and frequency of fire [13–15] and changes in herbivory by large mammals [14, 16] have also been considered important factors in causing an increase in woody plant density [17, 18].

We propose an alternative biophysical mechanism to explain woody thickening based upon changes in the soil-plant-atmosphere continuum resulting from a change in global atmospheric conditions. This mechanism is global in reach, appears consistent with a number of observations of trends in evaporation rates, run-off and soil moisture, and has several testable predictions, which we briefly discuss.

2. THE MODEL

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 [19].
(2) An increase in $[CO_2]_a$ has two effects. (a) it increases rates of photosynthesis of woody plants, typically of about 30% to 50% [20, 21]. Photosynthesis is enhanced more in woody shrubs (+45%) than grasses (+38%) or trees (+25%) in response to CO_2 enrichment [22]; and (b) leaf stomatal conductance of woody plants is decreased by about 20% [23]. C4 grasses show a smaller stomatal and photosynthetic response to CO_2 enrichment than C3 plants such as shrubs and trees.

(3) The growth rate of trees and shrubs is increased by enrichment of $[CO_2]_a$ because of an enhanced rate of photosynthesis [21]. Importantly, the proportional increase in tree growth is larger under xeric than mesic conditions [20].
(4) Pan evaporation rates have declined globally [24]. Across Australia, for example, the decline in pan evaporation rates for the past four decades has been between 1 and 3 mm per year [25, 26].
(5) Because of decreased rates of evaporation and g_s, soil moisture content is larger in the short-to-medium-term and this leads to increased tree density.

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 reveal increased values. Second, run-off data should show an increase where woody thickening is occurring. Third, enriched CO_2 experiments should reveal an enhanced plant water status. These predictions are discussed later.

3. MATERIALS AND METHODS

We explored long-term climate data sets for southern Africa to determine whether site wetness has been increasing. We are not aware of any analyses of such data from southern Africa to-date and therefore chose this location to add to the analyses available for Europe, America, Australia, and New Zealand [25, 27]. We analysed records from evaporation pans, rainfall, and run-off at these sites. Using reports from the literature and aerial photography interpretation, we tested whether woody cover has been increasing at selected sites throughout the arid and semiarid regions of southern Africa, in agreement with trends reported globally.

3.1. MODIS LAI product

We explored trends in the leaf area index for large areas (>10 km^2) with a known history of woody biomass increase using the MODIS LAI product. We used 7 years of the MODIS 8-day 1 km Collection 4 (MOD15A2) composite LAI/FPAR product [28] for the period from February 2000 to December 2006 from the NASA Distributed Active Archive Centre. These data were extracted using the MODIS reprojection tool and imported into IDRISI image processing package to create a 7-year data stack. The geocodes for the USA (Jornada LTER, NM) site were entered into the GIS, 8-day LAI values for the region were extracted, and a single 8-day mean was calculated for each year.

4. RESULTS AND DISCUSSION

In contrast to the expectation that global warming would result in increased evaporation, a decrease in pan evaporation rates has been recorded for the northern hemisphere, Australia, and New Zealand [24, 25]. This result is confirmed in the present study for several arid and semiarid regions of southern Africa (Figure 1) in the absence of any discernable trend in annual precipitation (Figure 2). In water-limited ecosystems, decreasing pan evaporation rates can best be explained by decreased wind speed [29] and decreased solar radiation receipt at ground level because of increased cloud cover and atmospheric aerosol content.

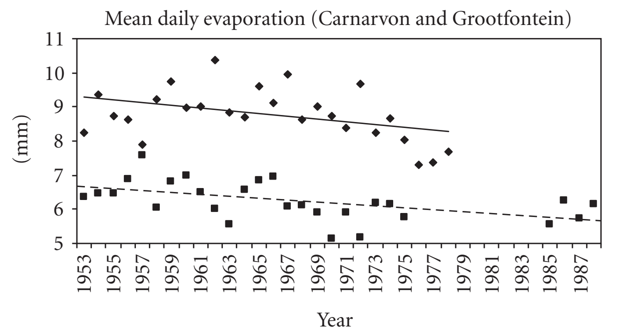

Figure 1: Trends in evaporation for two stations in South Africa. Data were provided by the Hydrological Information System of the South African Department of Water Affairs and Forestry.

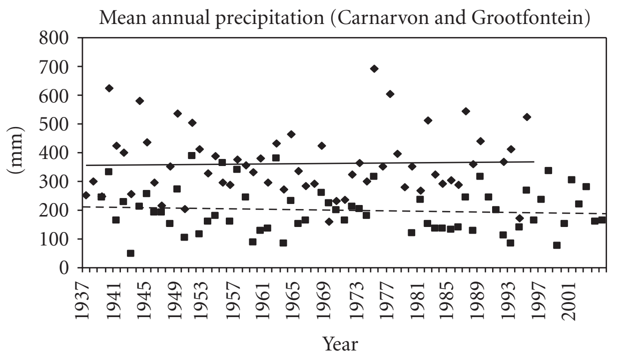

Figure 2: Trends in precipitation for the stations in Figure 1.Data were provided by the Hydrological Information System of the South African Department of Water Affairs and Forestry.

Vapour pressure deficit has decreased for water-limiting ecosystems of Africa, Australia, and the Indian subcontinent [30]; this is another measure of a decreasing pan evaporation rate. Because of a decrease in evaporative demand, we must predict that in the absence of a change in rainfall, either soil moisture content must be larger in the short-term or excess moisture is being lost through a larger rate of run-off. In the longer-term, we expect enhanced rates of vegetation water use that has increased its density in response to the earlier rise in soil moisture content. The prediction that increased run-off as a consequence of climate change is supported from both observational and simulation studies [31, 32]. 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 [33] through the observed response of g_s to $[CO_2]_a$, [20, 22].

There is evidence of global soil moisture increasing [34, 35], with positive soil moisture trends observed during the

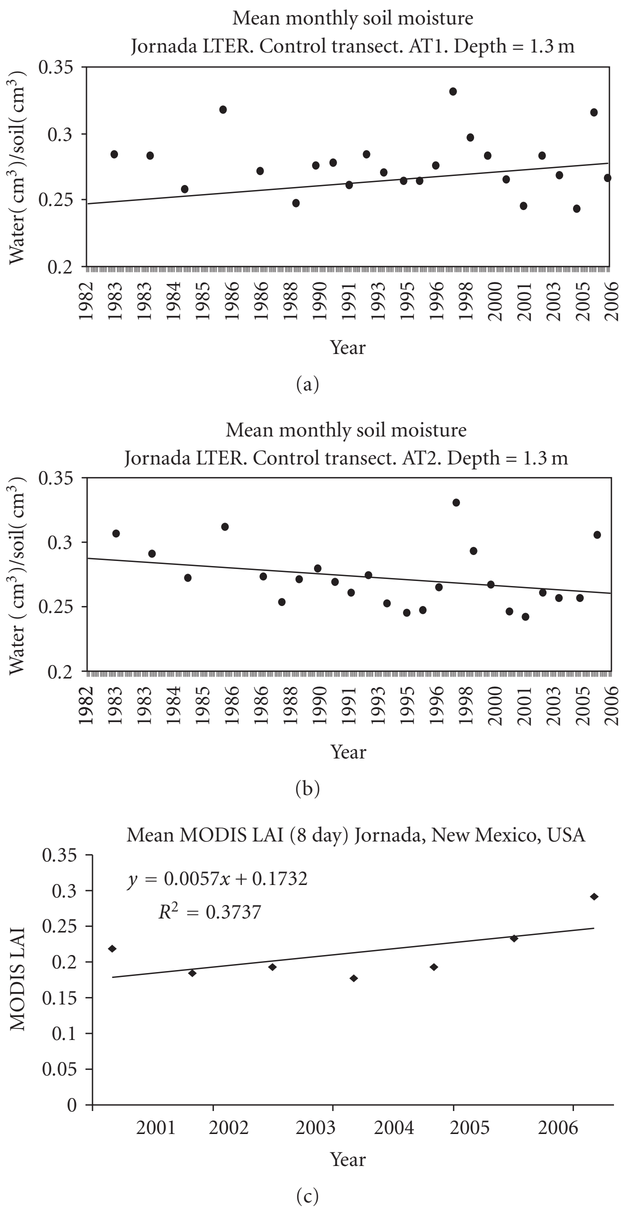

Figure 3: Trends in deep soil moisture at the Jornada LTER site. Access tube 1(AT1) is located in a playa which has low woody shrub cover, while the area around access tube 2 (AT2) is encroached by *Prosopis glandulosa*. Increased MODIS LAI was observed at sites where woody encroachment was occurring.

20th century in the Ukraine, Mongolia and the western USA, for example [36, 37]. 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 [35]. For arid and semiarid regions of the southern hemisphere, however, evidence of increases in soil moisture is limited. Elevated moisture levels across land-use gradients have been recorded in grassed deep sand-dunes of the southern Kalahari [38] and this has promoted the success of C3 shrubs and trees at these locations. Similarly in an encroached area at the Jornada LTER site in New Mexico, where soil moisture has been recorded monthly since 1982, soil moisture at a depth of 1.3 m has increased in the non-wooded playa but decreased in the areas encroached by *Prosopis glandulosa* with a concomitant increase in MODIS LAI (Figure 3). Such increased soil moisture where woody thickening has yet to occur is expected in the short-term, whilst a decline in soil moisture where woody thickening has occurred is expected in the longer-term.

In many field CO_2 enrichment studies, the soil moisture content below woody vegetation is increased in response to CO_2 enrichment even when the leaf area index was increased [39, 40]. Such a response is predicted from the model proposed.

A second prediction from this model is that a reduced g_s in response to CO_2 enrichment and a concomitant increase 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 [41]. Reference [42] reviews much of the literature and shows that improved water status is frequently observed in CO_2 enrichment studies. These differences were larger during drought than wetter conditions, indicating the importance of this effect during periods of low water availability [43].

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 g_s arising from increased $[CO_2]_a$. In support of this prediction is the long-term increase in WUE of trees that has been reported over the past 100 years [44]. In addition, drier sites will be more sensitive to inter-annual rainfall than wetter sites and the response of above-ground net primary production (and hence woody thickening) will be larger in low rainfall sites, so we might expect a significantly larger degree of woody thickening here than in mesic regions [45].

Clearly, we have a simple yet powerful explanation for the trend of increasing woody thickening observed in arid and semiarid regions over the past 50–100 years. As pan evaporation rates have declined, the availability of soil moisture has increased, effectively equivalent to increased rainfall. This has resulted in an increased ecosystem-scale woody thickening. Superimposed on this is the decrease in g_s resulting from increased atmospheric $[CO_2]_a$ [21, 22] which can also reduce leaf-scale transpiration rates. We conclude that this conceptual model and its three predictions are strongly supported by both experimental and simulation studies.

REFERENCES

[1] T. G. O'Connor and V. R. T. Crow, "Rate and pattern of bush encroachment in eastern Cape savanna and grassland," *African Journal of Range & Forage Science*, vol. 16, no. 1, pp. 26–31, 1999.

[2] M. T. Hoffman and T. G. O'Connor, "Vegetation change over 40 years in the Weenen/Muden area, KwaZulu-Natal: evidence from photo-panoramas," *African Journal of Range & Forage Science*, vol. 16, no. 2-3, pp. 71–88, 1999.

[3] R. J. Fensham, R. J. Fairfax, and S. R. Archer, "Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna," *Journal of Ecology*, vol. 93, no. 3, pp. 596–606, 2005.

[4] L. Zhou, C. J. Tucker, R. K. Kaufmann, D. Slayback, N. V. Shabanov, and R. B. Myneni, "Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999," *Journal of Geophysical Research*, vol. 106, no. D17, pp. 20069–20084, 2001.

[5] H. L. Spiecker, K. Mielikainen, M. Kohl, and J. P. Skovsgaard, *Growth Trends in Europe*, Springer, Berlin, Germany, 2003.

[6] D. M. J. S. Bowman, A. Walsh, and D. J. Milne, "Forest expansion and grassland contraction within a *Eucalyptus* savanna matrix between 1941 and 1994 at Litchfield National Park in the Australian monsoon tropics," *Global Ecology and Biogeography*, vol. 10, no. 5, pp. 535–548, 2001.

[7] W. H. Burrows, B. K. Henry, P. V. Back, et al., "Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications," *Global Change Biology*, vol. 8, no. 8, pp. 769–784, 2002.

[8] T. G. O'Connor and G. J. Bredenkamp, "Grasslands," in *Vegetation of South Africa*, R. M. Cowling, D. M. Richardson, and S. M. Pierce, Eds., pp. 215–257, Cambridge University Press, Cambridge, UK, 1997.

[9] K. G. Roques, T. G. O'Connor, and A. R. Watkinson, "Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence," *Journal of Applied Ecology*, vol. 38, no. 2, pp. 268–280, 2001.

[10] H. Walter, *Ecology of Tropical and Subtropical Vegetation*, Oliver & Boyd, London, UK, 1971.

[11] B. H. Walker and I. Noy-Meir, "Aspects of the stability and resilience of savanna ecosystems," in *Ecology of Tropical Savannas*, B. J. Huntley and B. H. Walker, Eds., pp. 556–590, Springer, Berlin, Germany, 1982.

[12] B. H. Walker, D. Ludwig, C. S. Holling, and R. M. Peterman, "Stability of semi-arid savanna grazing systems," *Journal of Ecology*, vol. 69, no. 2, pp. 473–498, 1981.

[13] R. J. Scholes and S. R. Archer, "Tree-grass interactions in savannas," *Annual Review of Ecology and Systematics*, vol. 28, pp. 517–544, 1997.

[14] F. Van Langevelde, C. A. D. M. Van De Vijver, L. Kumar, et al., "Effects of fire and herbivory on the stability of savanna ecosystems," *Ecology*, vol. 84, no. 2, pp. 337–350, 2003.

[15] W. S. W. Trollope and N. M. Tainton, "Effect of fire intensity on the grass and bush components of the eastern Cape Thornveld," *Journal of Grassland Society of South Africa*, vol. 3, pp. 37–42, 1986.

[16] S. J. McNaughton, "The propagation of disturbance in savannas through food webs," *Journal of Vegetation Science*, vol. 3, no. 3, pp. 301–314, 1992.

[17] W. S. W. Trollope, "Fire behaviour," in *Veld Management in South Africa*, N. M. Tainton, Ed., pp. 217–228, University of Natal Press, Pietermaritzburg, South Africa, 1999.

[18] G. C. Stuart-Hill and N. M. Tainton, "Water utilization patterns around isolated *Acacia karroo* trees in the false Thornveld of the eastern Cape," *Journal of Grassland Society of South Africa*, vol. 6, pp. 195–204, 1989.

[19] C. D. Keeling, T. P. Whorf, M. Wahlen, and J. van der Plicht, "Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980," *Nature*, vol. 375, no. 6533, pp. 666–670, 1995.

[20] D. Eamus and R. Ceulemans, "Effects of greenhouse gases on the gas exchange of forest trees," in *The Impact of CO_2 and Other Greenhouse Gases on Forest Ecosystems*, D. Karnosky, R. Ceulemans, G. E. Scarascia-Mugnozza, and J. L. Innes, Eds., pp. 17–56, CABI Publishing, Wallingford, UK, 2001.

[21] D. Eamus and P. G. Jarvis, "The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests," *Advances in Ecological Research*, vol. 19, pp. 1–55, 1989.

[22] B. E. Medlyn, F.-W. Badeck, D. G. G. De Pury, et al., "Effects of elevated $[CO_2]$ on photosynthesis in European forest species: a meta-analysis of model parameters," *Plant, Cell & Environment*, vol. 22, no. 12, pp. 1475–1495, 1999.

[23] B. E. Medlyn, C. V. M. Barton, M. S. J. Broadmeadow, et al., "Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis," *New Phytologist*, vol. 149, no. 2, pp. 247–264, 2001.

[24] M. L. Roderick and G. D. Farquhar, "The cause of decreased pan evaporation over the past 50 years," *Science*, vol. 298, no. 5597, pp. 1410–1412, 2002.

[25] M. L. Roderick and G. D. Farquhar, "Changes in Australian pan evaporation from 1970 to 2002," *International Journal of Climatology*, vol. 24, no. 9, pp. 1077–1090, 2004.

[26] J. J. Sharples and M. F. Hutchinson, "Spatio-temporal analysis of climatic data using additive regression splines," in *Proceedings of International Congress on Modelling and Simulation (MODSIM '05)*, A. Zerger and R. M. Argent, Eds., pp. 1695–1701, Modelling and Simulation Society of Austrlaia and New Zealand, Melbourne, Australia, December 2005.

[27] M. L. Roderick and G. D. Farquhar, "Changes in New Zealand pan evaporation since the 1970s," *International Journal of Climatology*, vol. 25, no. 15, pp. 2031–2039, 2005.

[28] Y. Knyazikhin, J. V. Martonchik, R. B. Myneni, D. J. Diner, and S. W. Running, "Synergistic algorithm for estimating vegetation canopy leaf area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data," *Journal of Geophysical Research*, vol. 103, no. D24, pp. 32257–32276, 1998.

[29] M. L. Roderick and G. D. Farquhar, "A physical analysis of changes in Australian pan evaporation," Land & Water Australia Technical Report ANU49, The Australian National University, Canberra, Australia, 2006, http://www.rsbs.anu.edu.au/ResearchGroups/EBG/documents/TechnicalReport_PhysicEpan_2_001.pdf.

[30] R. R. Nemani, C. D. Keeling, H. Hashimoto, et al., "Climate-driven increases in global terrestrial net primary production from 1982 to 1999," *Science*, vol. 300, no. 5625, pp. 1560–1563, 2003.

[31] D. Labat, Y. Goddéris, J. L. Probst, and J. L. Guyot, "Evidence for global runoff increase related to climate warming," *Advances in Water Resources*, vol. 27, no. 6, pp. 631–642, 2004.

[32] J. L. Probst and Y. Tardy, "Long range streamflow and world continental runoff fluctuations since the beginning of this century," *Journal of Hydrology*, vol. 94, no. 3-4, pp. 289–311, 1987.

[33] N. Gedney, P. M. Cox, R. A. Betts, O. Boucher, C. Huntingford, and P. A. Stott, "Detection of a direct carbon dioxide effect in continental river runoff records," *Nature*, vol. 439, no. 7078, pp. 835–838, 2006.

[34] A. Robock, K. Y. Vinnikov, G. Srinivasan, et al., "The global soil moisture data bank," *Bulletin of the American Meteorological Society*, vol. 81, no. 6, pp. 1281–1299, 2000.

[35] A. Robock, M. Mu, K. Y. Vinnikov, I. V. Trofimova, and T. I. Adamenko, "Forty-five years of observed soil moisture in the Ukraine: no summer desiccation (yet)," *Geophysical Research Letters*, vol. 32, no. 3, p. L03401, 2005.

[36] A. F. Hamlet, P. W. Mote, M. P. Clark, and D. P. Lettenmaier, "Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States," *Journal of Climate*, vol. 20, no. 8, pp. 1468–1486, 2007.

[37] Y. Hirabayashi, S. Kanae, I. Struthers, and T. Oki, "A 100-year (1901–2000) global retrospective estimation of the terrestrial water cycle," *Journal of Geophysical Research*, vol. 110, no. D19, Article ID D19101, 23 pages, 2005.

[38] A. F. Van Rooyen, *Rangeland degradation in the southern Kalahari*, Ph.D. thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa, 1999.

[39] P. G. Cech, S. Pepin, and C. Körner, "Elevated CO_2 reduces sap flux in mature deciduous forest trees," *Oecologia*, vol. 137, no. 2, pp. 258–268, 2003.

[40] B. A. Hungate, M. Reichstein, P. Dijkstra, et al., "Evapotranspiration and soil water content in a scrub-oak woodland under carbon dioxide enrichment," *Global Change Biology*, vol. 8, no. 3, pp. 289–298, 2002.

[41] D. Eamus, C. A. Berryman, and G. A. Duff, "The impact of CO_2 enrichment on water relations in *Maranthes corymbosa* and *Eucalyptus tetrodonta*," *Australian Journal of Botany*, vol. 43, no. 3, pp. 273–282, 1995.

[42] S. D. Wullschleger, T. J. Tschaplinski, and R. J. Norby, "Plant water relations at elevated CO_2—implications for water-limited environments," *Plant, Cell & Environment*, vol. 25, no. 2, pp. 319–331, 2002.

[43] R. Tognetti, A. Raschi, and M. B. Jones, "Seasonal patterns of tissue water relations in three Mediterranean shrubs co-occurring at a natural CO_2 spring," *Plant, Cell & Environment*, vol. 23, no. 12, pp. 1341–1351, 2000.

[44] P. Hietz, W. Wanek, and O. Dünisch, "Long-term trends in cellulose δ^{13}C and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil," *Tree Physiology*, vol. 25, no. 6, pp. 745–752, 2005.

[45] T. E. Huxman, M. D. Smith, P. A. Fay, et al., "Convergence across biomes to a common rain-use efficiency," *Nature*, vol. 429, no. 6992, pp. 651–654, 2004.