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Ecophysiological controls over ecosystem water balance in an arid-land forest

K. Maseyk, E. Rotenberg and D. Yakir
Weizmann Institute of Science, Israel

Forest growth and function in semi-arid and arid conditions will depend on long term responses to the dry conditions, information that is not necessarily obtained from studies of episodic drought events in more mesic environments. Here we present results from four years of measurements of leaf and canopy scale biosphere-atmosphere exchange of CO_2 and H_2O from a *Pinus halepensis* forest in an arid environment. The forest is located in the Mediterranean climate zone on the edge of the Negev Desert, Israel, and therefore receives low annual precipitation (35 year average of ∼280mm, P/PET is ∼0.18) confined to about 5 months over the winter period. There is a long (6-8 month) completely rain-free period from late spring to early autumn, during which atmospheric water demand (daily maximum VPD) is usually above 3000 Pa. There is no access to ground water, and the annual total of evapotranspiration is very similar to total precipitation. Despite the harsh conditions, the average annual net ecosystem productivity for the last 4 years was 192 g C m^{-2}, which compares with the European average of 260 g C m^{-2}.

Soil water content is the prime driver for ecosystem activity. This results in the carbon uptake period being from December – June, peaking in Feb-March with leaf level rates of photosynthesis of 18-20 μmol m^{-2} s^{-1}. This represents a large temporal shift from both more mesic Mediterranean and temperate forest ecosystems, and results in a near inverse relationship of ecosystem activity with temperature. Imposed on this shift is a more constrained response of leaf phenology, with needle growth occurring from late March to October. Responding to a temperature cue, new needles appear earlier than in more northern environments, but the shift is not of the same extent as carbon uptake, resulting in a decoupling between the main period of carbon assimilation and needle growth. The development of new foliage each season is an important ecological variable in determining forest productivity, and this differential response of physiology

and phenology under these arid conditions represents an important feature that impacts on both the carbon and water cycles.

As needle expansion requires maintenance of cell turgor, a high degree of control over water loss is required during the growth phase, when water availability is low, demand is high and soil-leaf hydraulic conductance also declines. When the soil relative extractable water is above about 0.25, stomatal conductance (g_s) is between 0.05 – 0.5 mol m^{-2} s^{-1}, and is mainly a function of VPD. Below this level there is a sharp drop in g_s, which remains below 0.05 mol m^{-2} s^{-1} and is much less sensitive to the environmental conditions. Therefore leaf water potentials are maintained above a critical level, but carbon assimilation is compromised. A potentially important consequence of this high degree of stomatal control are low latent heat fluxes over summer and (monthly average) Bowen ratios in the order of 15 – 20.

A low level of on-going photosynthetic activity through the summer months (primarily in the early morning and late afternoon) sustains needle growth, but not total ecosystem carbon requirements, and the ecosystem becomes a net source of carbon to the atmosphere. However, these losses may be compensated by the fact that at the start of the wet season a complete canopy is present, including the new needles of highest photosynthetic capacity. Therefore optimal rates of carbon fixation can occur upon recharge of soil water, enabling the relatively high levels of productivity to be obtained.