The influence of soil moisture on stomatal conductance responsiveness to CO_2

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Abstract
Plants have the ability to reduce their transpirational water loss under high CO_2 conditions by changing their stomatal conductance (gsmax). Changes in stomatal conductance can have severe effects on local hydrology; therefore it is important to understand how plants have adapted to the industrial rise in CO_2 and how soil moisture influences the responsiveness of plants to CO_2. This paper focuses on the effects of different soil moisture regimes on stomatal conductance changes and how these changes may affect the environment.

Chapter 3: Stomatal conductance research and soil moisture

Chapter 1

An introduction to stomatal conductance

The importance of water

Water covers 71% of the Earth's surface, and is vital for all known forms of life. Only 2.5% of the Earth's water is fresh water, and 98.8% of that water is in ice and groundwater. Less than 0.3% of all freshwater is in rivers, lakes, and the atmosphere, and an even smaller amount of the Earth's freshwater (0.003%) is contained within biological bodies and manufactured products (Gleick 1993). Water on Earth moves continually through the hydrological cycle (Figure 1) of evaporation and transpiration (evapotranspiration), condensation, precipitation, and runoff, usually reaching the sea (LingLing 2013, national weather service Jetstream project). Safe drinking water is essential to humans and other life forms even though it provides no calories or organic nutrients. Water plays an important role in the world economy, as it functions as a solvent for a wide variety of chemical substances and facilitates industrial cooling and transportation. Approximately 70% of the fresh water used by humans goes to agriculture (MDG report). It is therefore understandable that we want to understand the behaviour of water on our planet and get a clear overview on all the different water fluxes.

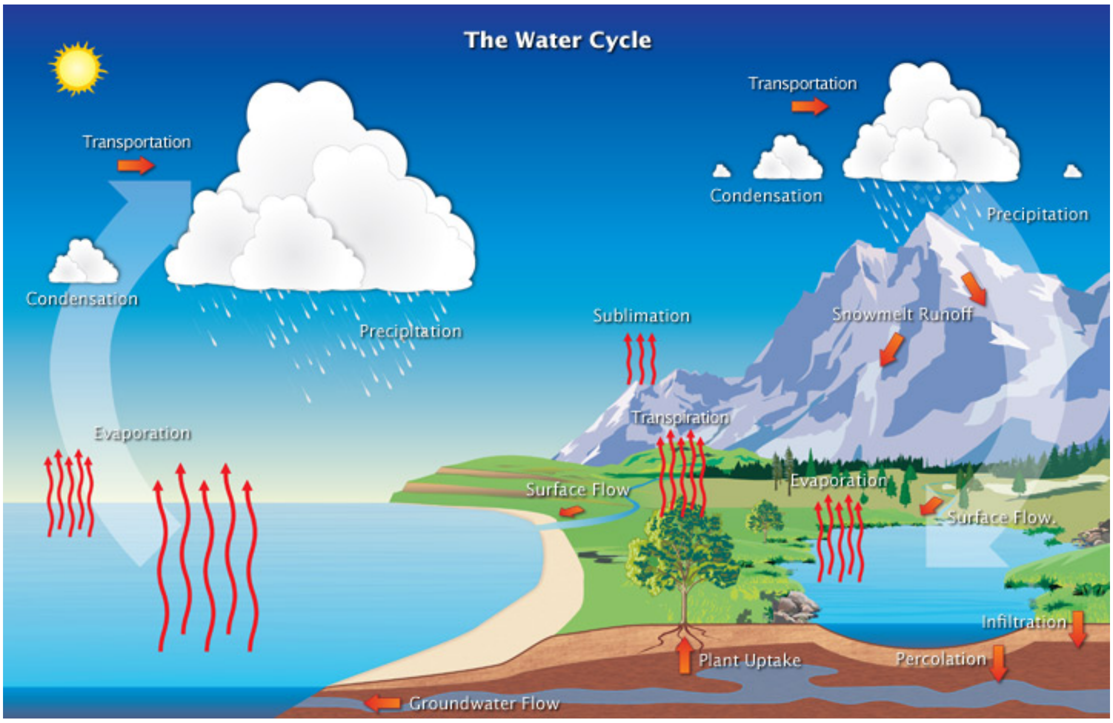

Figure 1. Water moves through Earth's systems in a cyclic fashion taking many forms as it travels. This process is known as the Hydrologic or Water Cycle. Source: National Weather Service Jetstream project (NASA, 2013)

Transpiration

As the illustration shows, water moves over, above and below the earth in a lot of different ways. For example, it can evaporate directly from the ocean or a lake, condensate and come down to the earth's surface as rain. The majority of the water flux from the earth's land surface to the atmosphere however, passes through the tiny conductive pores (stomata) in the leaves of land plants, through a process called transpiration (Kurschner et al. 1997). Plants take up CO_2 from the air for growth (photosynthesis) through the stomata on their leaf surface, but loose water through these pores at the same time (Figure 2).

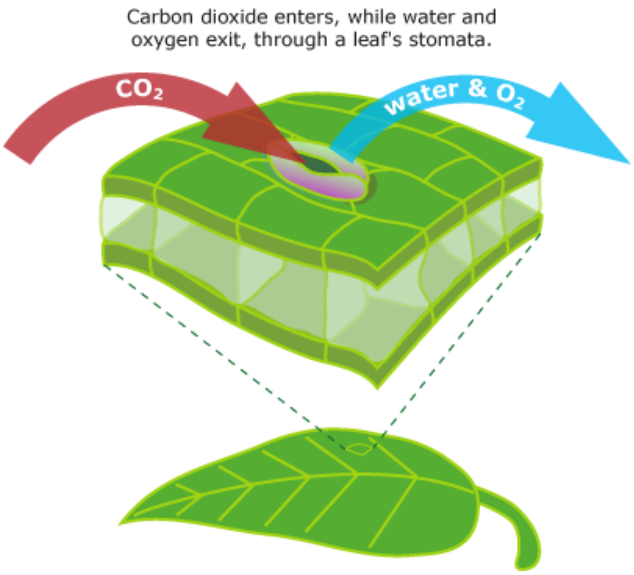

Figure 2. Carbon dioxide enters, while water and oxygen exit. (Berkeley, 2013)

The CO_2 problem

The concentration of carbon dioxide (CO_2) in Earth's atmosphere has reached 400 ppm (parts per million) as of May 2013 and rose by 2.0 ppm/yr during 2000–2009 and faster since then (Tans and Keeling, 2013). This current concentration is substantially higher than the 280 ppm concentration present in pre-industrial times, with the increase largely attributed to anthropogenic sources. Carbon dioxide is used in photosynthesis and is also a prominent greenhouse gas. Despite its relatively small overall concentration in the atmosphere, CO_2 is an important component of Earth's atmosphere because it absorbs and emits infrared radiation and thereby playing a role in the greenhouse effect. The present level is higher than at any time during the last 800 thousand years, and likely higher than in the past 20 million

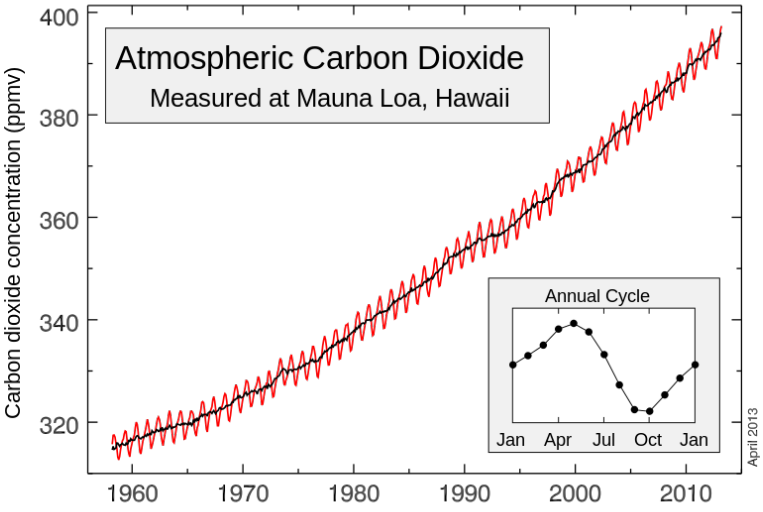

Figure 3. Atmospheric carbon dioxide concentrations (ESRL, 2013)

years (IPCC, 2007, NOAA). Figure 3 shows the rise in carbon dioxide concentrations in the atmosphere over the last decades.

CO_2, photosynthesis and stomata

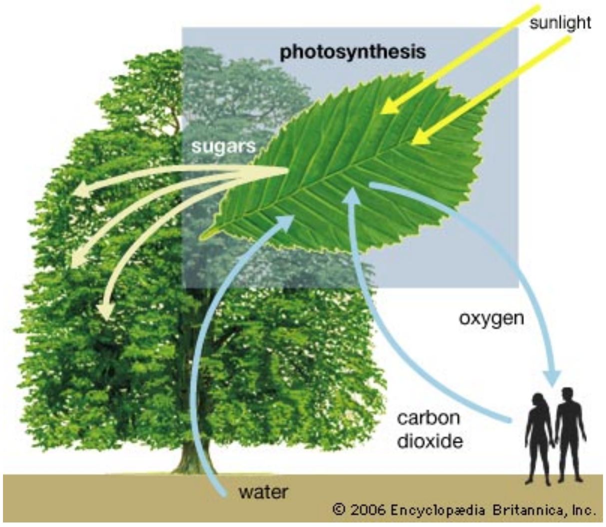

Figure 4 The proces of photosynthesis (Encyclopedia Brittanica, 2013)

Plants take up CO_2 from the air with their stomata and use it to create sugars in a process called photosynthesis. A very basic graphical representation of the process is shown in Figure 4. Rising CO_2 stimulates photosynthesis. Now that CO_2 is increasing, plants can reduce the conductance of their leaves to minimize water loss, while keeping up CO_2 uptake (Raven, 2002, Beerling et al., 2010). So at times when the atmosphere is carbon-dioxide-rich, plants can get away with having fewer stomata since each individual stoma will be able to bring in more carbon dioxide (Figure 5). During those high-carbon-dioxide times, plants with fewer stomata will have an advantage and will be common. On the other hand, when carbon dioxide levels are low, plants need many stomata in order to scrape together enough carbon dioxide to survive. During low-carbon-dioxide times, plants with more stomata will have an advantage and will be common (Wagner et al., 2004, Kurschner et al., 1996).

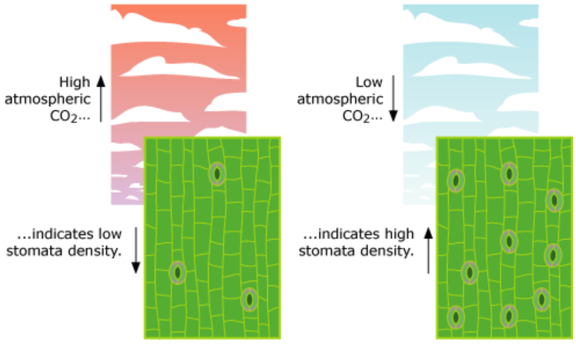

Figure 5. The relationship between atmospheric CO2 conentration and stomatal density (Berkeley 2013)

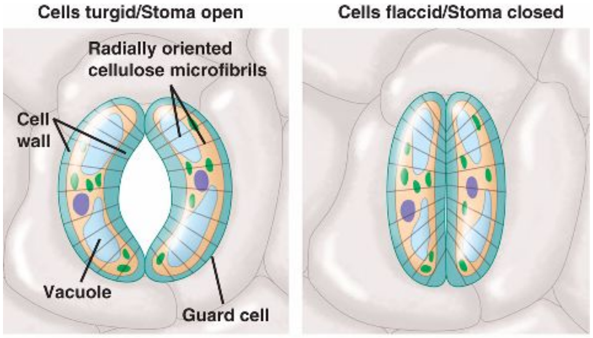

Figure 6. Open stomata (left) and closed stomata (right) (UIC, 2013)

The lowering of stomatal density by plants is a reaction to CO_2 that occurs over longer timescales. Over shorter timescales plants can alter their stomatal conductance by opening and closing their stomatal pores (Farguhal et al., 1978, Katul et al., 2010) (Figure 6).

Stomatal conductance research

In 1997 Kurschner et al. wrote a paper on CO_2 induced stomatal conductance changes. Studying species like oak (*Quercus petraea*) and Birch (*Betula pendula*, *Betula pubescens*) they found a significant decrease in the number of stomata on leafs over the anthropogenic rise of atmospheric CO_2. They predict that the species may reach their response limit at a CO_2 concentration of 400 ppmv. Earth’s atmosphere reached this concentration in May 2013. A quick overview of the results can be found in Figure 7.

In 2011 Lammertsma et al. conducted research in Florida on the effect CO_2 has on stomatal conductance (Figure 8). Despite that needle and broadleaved species seemed to respond differently to rising CO2, they reduced transpiration equally. The researchers concluded that plants will continue to adapt to at least double today's CO_2 concentration. This will result in a 40% reduction of transpiration from Florida forests at the end of this century and probably for most forests worldwide.

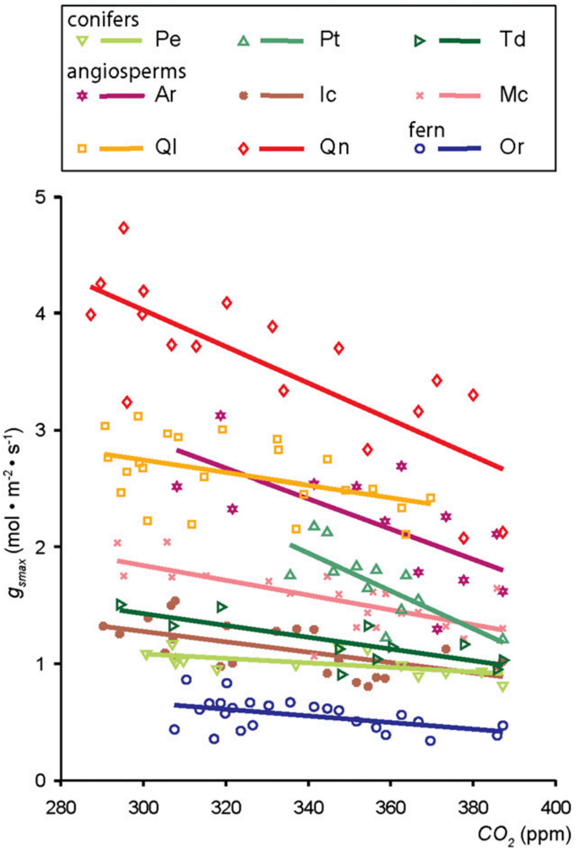

Figure 8. Species-specific relation between gsmax and CO_2 over the past 150 y. Symbols are average gsmax (mol·m−2·s−1) for each species per CO_2 level (ppm) studied (n = 160), and accompanying year A.D. Solid lines show linear regressions between CO_2 and gsmax for each species (Lammertsma et al. 2011).

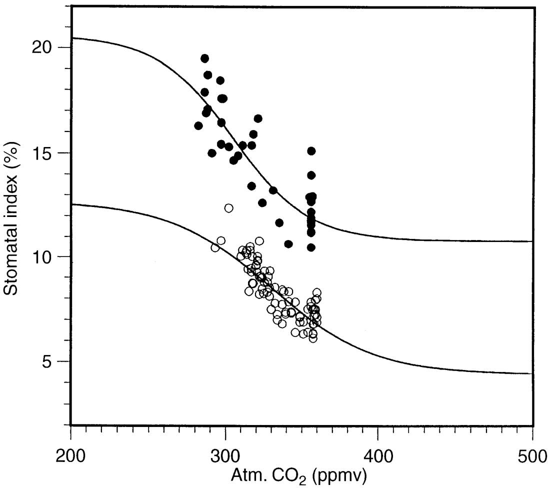

Figure 7. Modelled response curves for mean stomatal indices of the Durmast oak (Quercus petraea) and European tree birches (Betula pendula, Betula pubescens) as a sigmoid function of changing atmospheric CO_2 concentration, fitted with mean stomatal indices for leaves collected over the past 110 years (Kurschner et al. 1997).

Potential environmental impacts

The changes in stomatal conductance and transpiration could have large consequences for the hydrological cycle and climate. It already causes an increase in continental runoff and less transpiration may increase river flow and alter rainfall patterns. Moreover, transpiration leads to a surface cooling, comparable to the effect of sweating on a hot day. Reduced transpiration by plants adapting to rising CO_2 might therefore lead to a stronger surface temperature increase than currently expected (Gedney et al. 2006).

Unanswered questions

Lammertsma et al. have done extensive stomatal conductance research in Florida in 2011. Florida conifers, angiosperms and fern species show a comparable response to CO_2, suggesting a uniform adaption in all plant types. Especially in drought stress sensitive areas, different adaption strategies can be expected. To what extent plant adaption differs amongst environments can be tested through response comparison for species within the same genus, but from diverse climate regions. Excellent test genera include oak (*Quercus*) and pine (*Pinus*), due tot their widespread distribution in different climate zones. Initial studies on *Pinus* indicate that besides the reduction in stomatal conductance in Florida pines over the past 150 years, comparable trends can be observed in *Pinus sylvestris* herbarium specimen collected in the Mediterranean. Furthermore, a preliminary comparison of this dry mountainous dataset to the water use efficiency of *Pinus sylvestris* tree rings from subarctic Scandinavia indicates that typical pine species are all highly sensitive to CO_2 rise. But to what extent this sensitivity differs, and whether this is also true for other common tree species, is yet to be determined.

Chapter two

Impacts of climate change on European forest types

Climate models and stomatal conductance

As we see on the news every day, the current rise in CO_2 and the climate change it is associated with has a huge impact on global environments and ecosystems. In order to come up with accurate predictions of future climate changes, researchers from around the globe are creating climate models that can help us understand how the different components of the global climate system react to rising CO_2 values. In order to make these predictions as accurate as possible a thorough understanding of the different components of the climate system is necessary. One of these components, which hasn't received all the attention it deserves is the transpiration of plants. In many climate models, transpiration is expressed in a single predetermined value but, as explained in the previous chapter, stomatal conductance and transpiration are highly correlated with atmospheric CO_2 values. It is therefore important to get a clear overview on how stomatal conductance changes work in different environmental settings.

For the rest of the paper I shall focus on the potential effect of soil moisture on stomatal conductance changes under rising atmospheric CO_2 values. This information is then used to make a prediction of changes in European forest ecosystems but in order to make predictions including stomatal conductance changes we need to know current views on the impact of future climate change on these ecosystems. The following part is adapted from a paper written by Lindner et al. in 2009.

Bioclimatic zonation

Climate change sensitivity and exposure differ between bioclimatic zones and forest types in Europe. The bioclimatic map of Europe was used as reference classification; the top-level hierarchy of this bioclimatic classification is four macrobioclimates delimited by means of current climatic parameters and vegetation characteristics. European forests cover three major macrobioclimates: Boreal, Temperate and Mediterranean. Each of them and their subordinate units or bioclimates is represented by a characteristic group of forest formations. Temperate macrobioclimate was divieded to reflect the effect of continentality and used four bioclimatic zones to structure this review – Boreal, Temperate Oceanic, Temperate Continental and Mediterranean. In addition mountainous regions were separately considered to better represent mountain specific processes and impacts.

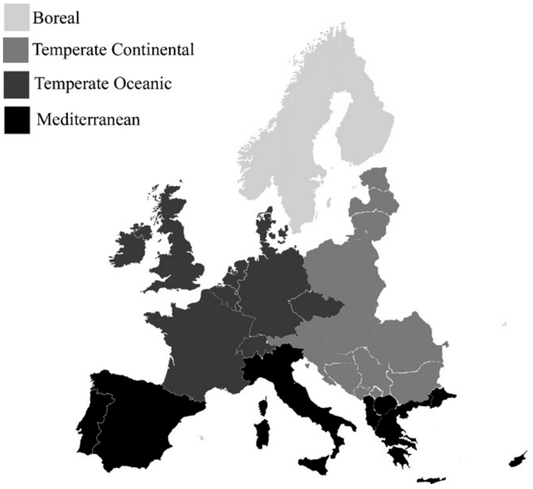

Figure 8. Principle allocation of European countries to bioclimatic zones. Many countries span across different zones and results of neighbouring zones should also be considered (Linder et al. 2009)..

Figure 8 shows the simplifying assignment of European countries to bioclimatic zones.

The boreal zone

The Taiga or boreal zone is the world's largest land biome, and makes up 29% of the world's forest cover. The largest areas are located in Russia and Canada. The Taiga is the terrestrial biome with the lowest annual average temperatures after the tundra and permanent ice caps. The taiga or boreal forest has a subarctic climate with very large temperature range between seasons, but the long and cold winter is the dominant feature. The forests of the taiga are largely coniferous, dominated by larch, spruce, fir, and pine. The woodland mix varies according to geography and climate.

Figure 9. Boreal forest (Art, 2013)

Expected changes

For the Boreal zone, temperatures are expected to increase by 3.5 tot 5 C with higher increase during winter (4-7) than in summer (3-4). Significant increases in yearly precipitation (up to 40%) are predicted and winters are projected to become wetter. Short growing seasons, low summer temperatures and short supply of nitrogen limit the productivity of boreal forests. The projected change in temperature will prolong the growing season, enhance the decomposition of soil organic matter and increase the supply of nitrogen. This may further enhance forest growth, consequent timber yield and the accumulation of carbon in the biomass. However, in areas with reduced precipitation in the southern Boreal, the potential increase in productivity could be reduced or offset due to water limitations. Milder winters may reduce winter hardening in trees, increasing vulnerability to frost e.g. in oak stands in south-western Finland Warmer and wetter winters negatively affect logging operations on wet soils. Tree species distributions may change and broad- leaved deciduous trees are expected to expand northwards. Forest damage by wind and snow are projected to increase.

Temperate Oceanic Zone

The maritime climate is affected by the oceans, which help to sustain somewhat stable temperatures throughout the year. In temperate zones the prevailing winds are from the west, thus the western In the Northern hemisphere, characteristic dominant broadleaf trees in this biome include oaks (*Quercus* spp.), beeches (*Fagus* spp.), maples (*Acer* spp.), and birches (*Betula* spp.). The term "mixed forest" comes from the inclusion of coniferous trees as a canopy component of these forests. Typical coniferous trees include: Pines (*Pinus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.). In some areas of this biome the conifers may be a more important canopy species than the broadleaf species.

Figure 10. Temperate forest (Climatic, 2013)

Expected changes

Annual mean temperature increases are projected to be 2.5– 3.5 8C, except for the UK and Ireland with 2–3 8C. Summers are likely to be dryer and hotter (up to 4 8C increase). Extreme events such as storms, floods and droughts are projected to become more harmful.

Temperature increase will have a positive impact on forest growth in northern and western parts (i.e. less water-limited areas) and a negative impact on southern and eastern parts (i.e. water-limited regions). In the southern parts of the region droughts are the main constraint of forest growth and productivity. Temperature increase may have strong impacts on forest productivity and the competitive relationships between tree species. A reduction in the number of species in the Atlantic areas is projected. In large areas of western and central Europe, more competitive deciduous trees may replace indigenous conifers.

Temeperate Continental Zone

Forest composition in the temperate continental zone is similar to the forest composition in the temperate oceanic zone. Characteristic dominant broadleaf trees in this biome include oaks (*Quercus* spp.), beeches (*Fagus* spp.), maples (*Acer* spp.), and birches (*Betula* spp.). The term "mixed forest" comes from the inclusion of coniferous trees as a canopy component of these forests. Typical coniferous trees include: Pines (*Pinus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.). In some areas of this biome the conifers may be a more important canopy species than the broadleaf species.

Figure 11. Temperate forest (123RF, 2013)

Expected changes

The annual mean temperature increase is projected to be in the order of 3–4 8C and up to 4.5 8C in the Black Sea Region. Annual mean precipitation is expected to increase by up to 10% mainly in winter, while summer precipitation is projected to decline in several areas (up to -10%)

In this bioclimatic zone, forest production is mainly constrained by water availability and decreasing annual precipitation or changes in inter- and intra-annual distribution will result in stronger water limitations than today. Production is likely to decrease at sites vulnerable to water stress and to increase where the increased evaporative demand under the elevated temperature is balanced by an increase in precipitation. Impacts on individual species can be either positive or negative, depending on site conditions and regional climatic changes. *Fagus sylvatica* is projected to face severe problems under increasing temperatures. Milder winters may reduce winter hardening in trees, increasing their vulnerability to frost.

Mediterranean zone

The Mediterranean Basin is the largest of the world's five Mediterranean forests, woodlands, and scrub regions. It is home to a number of plant communities, which vary with rainfall, elevation, latitude, and soils. Scrublands occur in the driest areas, especially areas near the seacoast where wind and salt spray are frequent. Shrublands are dense thickets of evergreen sclerophyll shrubs and small trees, and are the most common plant community around the Mediterranean. In some places shrublands are the mature vegetation type, and in other places the result of degradation of former forest or woodland by logging or overgrazing, or disturbance by major fires. Savannas and grasslands occur around the Mediterranean, usually dominated by annual grasses. Woodlands are usually dominated by oak and pine, mixed with other sclerophyll and coniferous trees. Forests are distinct from woodlands in having a closed canopy, and occur in the areas of highest rainfall and in riparian zones along rivers and streams where they receive summer water. Mediterranean forests are generally composed of evergreen trees, predominantly oak and pine. At higher elevations Mediterranean forests transition to mixed broadleaf and tall conifer forests similar to temperate zone forests.

Figure 12. Mediterranean forest (Wikimedia, 2013)

Expected Change

Annual mean temperatures are projected to increase in the order of 3–4 C (4–5 C in summer and 2–3 C in winter). Yearly rainfall is expected to drop by up to 20% of current annual precipitation (up to 50% less in summer), whereas winter precipitation is expected to increase. Changes in frequency, intensity, and duration of extreme events are likely to result in more hot days, heat waves, heavy precipitation events, and fewer cold days.

Rising temperatures and the projected decrease in rainfall will magnify drought risk. Photosynthesis will decrease during hot spells and biomass growth and yield are expected to decline. Even drought-adapted ecosystems are influenced by drought and increased drought is likely to lead to reduced plant growth and primary productivity and altered plant recruitment. Over the last 50 years, a temperature increase of 1.4 C (with stable annual precipitation) has already resulted in progressive replacement of European beech (*Fagus sylvatica*) by Holm oak (*Quercus ilex*) in the higher elevations of the Pyrenees. The main causes were reduced recruitment and increasing defoliation of beech. Moreover, other studies show that long-term drought stress reduced the productivity of beech forests at the southern range edge.

Chapter three

Stomatal conductance research and soil moisture

Experimental data

To answer the question whether soil moisture influences stomatal conductance under rising atmospheric CO_2 conditions, data from different environmental regions is needed. Although studies on this subject are scarce, some information can be found. Wertin et al. performed one of the most useful studies for this subject in 2012. They wanted to see how predicted future changes in air temperature and atmospheric CO_2 concentrations, coupled with altered precipitation, are expected to substantially affect tree growth.

For this experiment, they grew P*inus taeda (*loblolly pine*)* seedlings in closed treatment chambers at two sites, one in the northern (cool site) and one in the southern (warm site) portion of its range. The long-term mean growing season temperature differed by 5.5 °C between these sites. The sites were chosen because they are representative of the coolest and warmest growing season temperatures in the eastern portion of the current distribution of loblolly pine. Seedlings were exposed to four treatments at each site: ambient temperature, ambient [CO_2], high soil moisture availability*;* elevated temperature, elevated [CO_2], high soil moisture availability ambient temperature, ambient [CO_2], low soil moisture availability and elevated temperature, elevated [CO_2], low soil moisture availability.

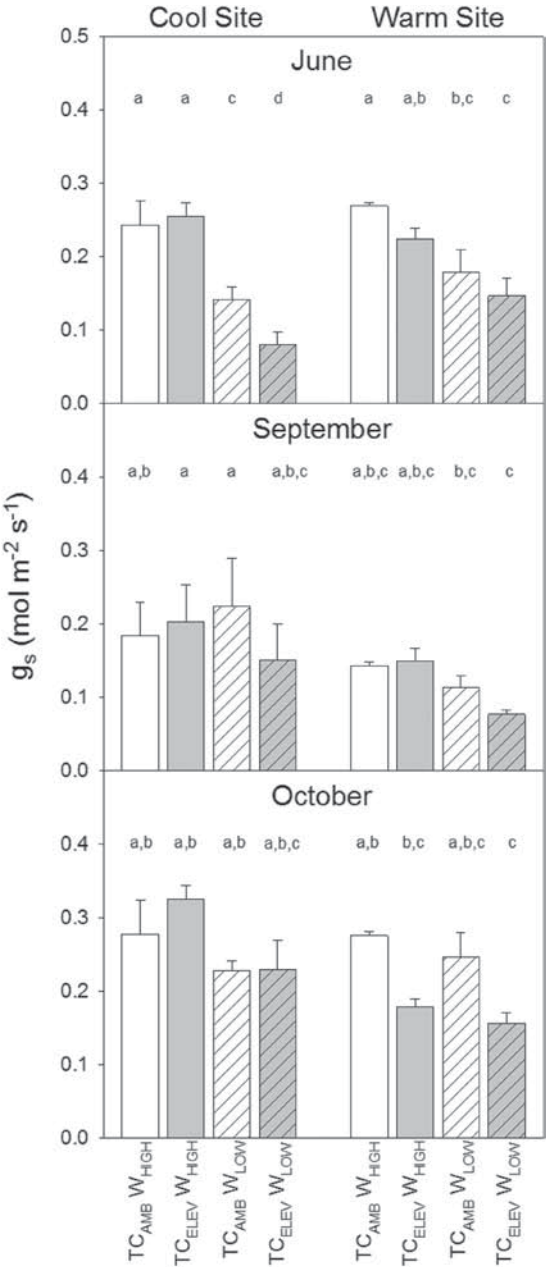

Figure 13. Results from the study performed by Wertin et al. in 2012

For all these sites stomatal comductance was measured on three different moments in the year (June, September and October). The results from this experiment can be found in Figure 13.

The left part of the figure represents the cool site of the experiment, while the right site is a representation of the results from the warm site. White bars are the ambient CO_2 and temperature treatments, dark bars are the elevated temperature and CO_2 treatments and the striped bars are the low soil moisture treatments.

First of all, the figure shows that elevated CO_2 seems to have the greatest effect on stomatal conductance on the warm sites. The conductance of the high CO_2 treatments is lower than the stomatal conductance of the seedlings of the low CO_2 treatments. Furthermore it seems that low soil moisture conditions seem to reduce the stomatal conductance even further. In all the growth experiments it seems that the lowest stomatal conductance values can be found in the elevated CO_2 and temperature treatment in combination with the low soil moisture treatments.

According to the statistics there was a significant effect of atmospheric treatment on stomatal conductance that was not affected by date, site, or soil moisture treatment. Averaged across all sites and measurement dates, stomatal conductance was significantly lower in the elevated CO_2 and temperature treatments compared with the ambient treatments.

The water treatment also significantly affected stomatal conductance at both sites. Averaged across both sites and atmospheric treatments, stomatal conductance was significantly greater in the high soil moisture treatments compared with the low soil moisture treatments. Putting al this together, it seems that low soil moisture reduces stomatal conductance even more than only elevated CO_2 and temperature does.

Although the overall stomatal conductance is lower on the warm site, it seems that the effect of soil moisture is the same for both the warm and the cool site. The difference in the stomatal conductance is the same. This could be an indication that geographical position does not matter in the stomatal conductance response of loblolly pine to different soil moisture, CO_2 and temperature changes.

In conclusion, elevated CO_2 and low soil moisture reduce stomatal conductance, but the response is the same for trees from different sites. Location does not seem to have an impact on the severity of the environmental changes.

Long term palaeo data

The previous study is an example of how different environmental factors influence stomatal conductance in a short-term experimental setting. This gives an indication how plants may react to future changes in climate and environmental factors. But to fully understand the effect of future changes, we need to look in to the past and search for actual real life changes to climate change, preferably data spanning the current anthropogenic rise in atmospheric CO_2. It is however, very difficult to find stomatal conductance data from this period, for it is a relative new area of research.
One of the things that can be used as an indicator for stomatal conductance is the water use efficiency. These studies have been conducted for the preferred timeframe and are therefore useful for our understanding of stomatal conductance changes and environmental feedbacks.

Water use efficiency

One study, performed by Maesyk et al. in 2011 examined the interactions of intrinsic water-use efficiency with environmental conditions in *Pinus Halapensis*. To do this they studied trees from three sites, located across a steep precipitation gradient in Israel with otherwise similar large-scale climatology. The three sites chosen were located in the Mediterranean climate zone along a north-south rainfall gradient in Israel. Mount Carmel (annual rainfall: 700 mm), Judean Hills (annual rainfall: 530 mm) and the Yatir Forest (annual rainfall: 280 mm). Results from this research can be found in Figure 13.

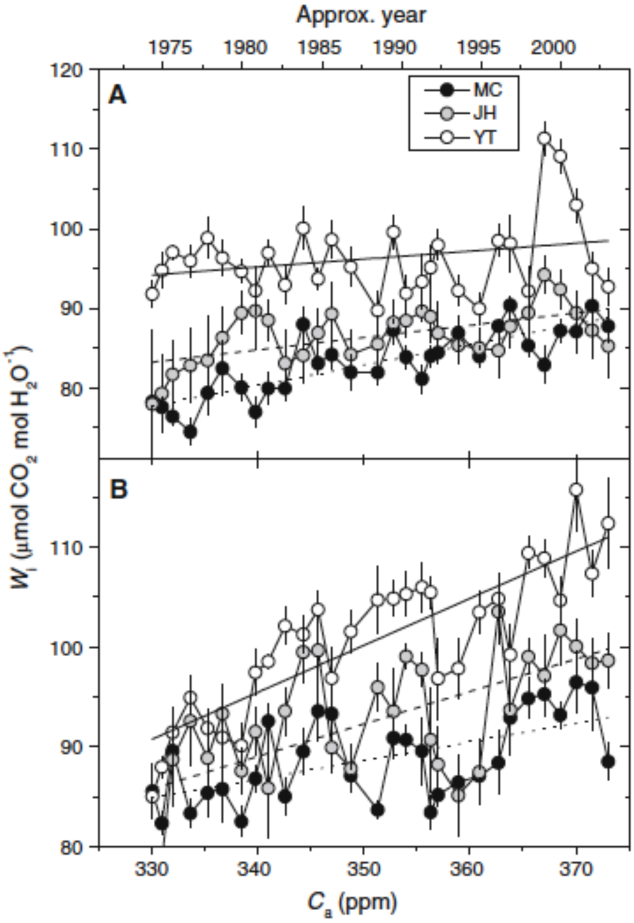

Figure 13. Results from the study performed by Maseyk et al. in 2011.

As the authors state in their discussion, a complex pattern was observed: while average water use efficiency increased with site aridity, the sensitivity of water use efficiency to carbon dioxide decreased with increasing aridity in earlywoord and increased with aridity in latewood. The authors discuss that this pattern is due to a shift in gas excahgen behaviour from regulation aimed at optimising carbon uptake under mild drought stress and increasing water use efficiency under more severe drought.

Chapter 4

Discussing future stomatal conductance research

It is clear that soil moisture has an effect on changes in stomatal conductance, but does it work the other way around as well? To what extent do changes in stomatal conductance influence the water cycle? The following part is adapted from Wassen et al. (2013) and contains hypotheses on the effect of stomatal adaption to the carbon-water cycle.

Perspective on the role of terrestrial vegetation and adaptation in carbon–water feedbacks

The stomatal responses reported before suggest that plant adaption to rising CO_2 might have consequences at larger scales. The downregulation of stomatal conductance may influence the freshwater cycle, especially when water is limited, as the vegetation will use less water. This hypothesis is supported by independent empirical data from river runoff that suggest that continental-scale evapotranspiration has decreased over the past century (Gedney et al. 2006). In ecosystems with limited water availability, the stomatal plant response is expected to lead to increased productivity, due to increased water use efficiency under elevated CO_2 (e.g. Huang et al. 2007). Figure 14 is a hypothetical diagram of potential feedbacks between the C cycle and the water cycle. Rising atmospheric CO_2 concentrations enhance primary productivity (C fertilization) but at the same time trigger structural adaptations of plants that diminish their stomatal conductance and transpiration. This negative feedback may alter the regional freshwater cycle, leading to enhanced soil water availability and enhanced primary productivity as long as the system is water-limited. In turn, enhanced primary productivity feeds back negatively to atmospheric CO_2 concentrations. However, the attenuation of atmospheric CO_2 increase is a relatively slow and global process, and anthropogenic CO_2 emissions are likely to exceed CO_2 uptake by plants. Also, if primary productivity of vegetation increases, increased total leaf area may offset the reduction in transpiration from leaves. Then, the negative effect of increased atmospheric CO_2 via stomata on transpiration is expected to outweigh the positive effect of primary productivity.

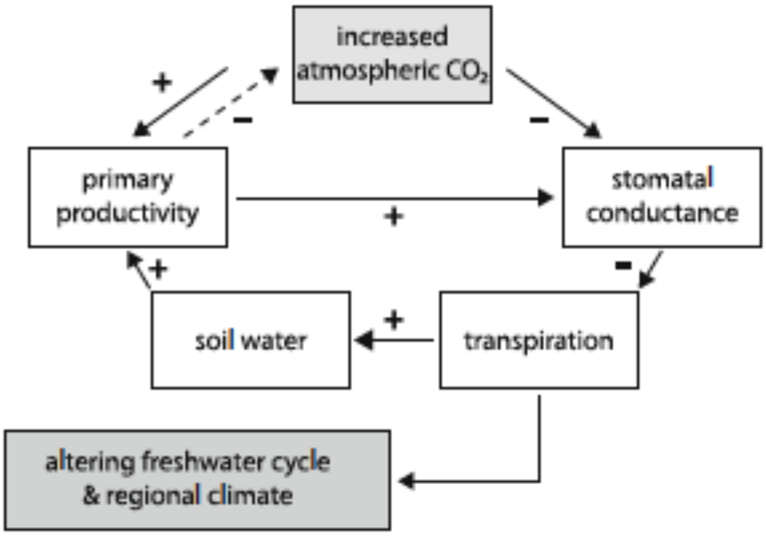

Figure 14 shows relationships and feedbacks between environmental variables and plant processes after an increase in atmospheric CO2 (Wassen et al. 2013).

As a result, vegetation responses to rising CO_2 might exert a strong biological control on the regional climate system via the water cycle, which may even propagate to the global scale via the C cycle. Interrelationships between the C cycle and the water cycle exert both positive and negative feedbacks, with the net feedback effect depending on different environmental factors that limit primary productivity, such as light, nutrients and water. The importance of the landscape scale for such feedbacks is evident, especially in the case of large-scale anthropogenic land use changes, such as reforestation, deforestation or large bio-fuel plantations.

Implications for European forest types

As the information above clarifies we do not yet have a clear overview on the role of terrestrial vegetation and adaption in carbon-water feedbacks. As the experiments in the previous chapters have shown, it seems that the combination of drought and rising CO_2 has an amplified effect on stomatal conductance and transpiration changes.

Boreal zone

As explained in the first chapter, the Boreal Zone is expected to become wetter. This can mean that stomatal conductace changes may not have a severe effect on the environment, because the system is not limited in water. Furthermore, increased soil moisture and atmospheric CO_2 may increase primary productivity, which can have a positive effect on stomatal conductance.

For this forest type it is important to get a clear understanding in the scope of the effect of CO_2 on stomtal conductance, for a reduction in stomatal conductance and an increase in soil moisture will definitely lead to excessive run off in these areas.

Temperate zones

The biggest changes for these systems lie in the water-limited areas. Here, the limited water availability in combination with higher atmospheric CO_2 values cause a decrease in stomatal conductance, but as the diagram above indicates, this could lead to a reduction in transporation, which could have a positive effect on the soil moisture conditions

Mediterranean zone

The biggest problem for these forest types is drought. The combination of drought and rising atmospheric CO_2 will cause a reduction in stomatal conductance. This could have a positive influence on soil moisture, but more research is needed to see if this positive effect is visible in very dry areas.

Future research

There are still many uncertainties regarding the effect of soil moisture regimes on stomatal conductance and on the feedback of stomatal conductance change to soil moisture regimes. One of the most important things to clarify is whether the potential positive effect of stomatal closure on soil moisture regimes in dry areas is significant if temperatures keep rising and the amount of annual precipitation declines. On the other hand, in areas that are getting wetter and wetter due to increased precipitation patterns, it is important to get an understanding on the increase in transpiration and whether this keeps soil moisture levels under control in wet areas.

If we want to understand how these systems function and what role transpiration plays, more research is needed. Stomatal conductance research on the same species in different environmental settings could provide clues regarding the feedback system between soil and atmosphere in areas where precipitation patterns are changing. This can provide us with information on the adaption of land plants to current rising atmospheric CO_2 and the role of soil moisture in this complex system of feedbacks.

Literature

123RF (2013), Mixed fores in autumn [online picture] from
http://climatic.inforef.be/palyno/14/014_en.htm

Art (2013), Finland, Aulanko, Scandinavian Forest [online picture] from
http://eu.art.com/products/p12234783-sa-i1607320/posters.htm

Berkeley (2013), Understanding evolution: leaves with microscopic mouths [online afbeelding] van
http://evolution.berkeley.edu/evolibrary/article/mcelwain_02

Climatic (2013), The virtual climatic laboratory [online picture] from
http://climatic.inforef.be/palyno/14/014_en.htm

Encyclopdia Brittanica (2013) photosynthesis [online picture] from
http://kids.britannica.com/elementary/art-88647/Green-plants-such-as-trees-use-carbon-dioxide-sunlight-and

ESRL (2013), Earth system research laboratory: Global monitoring division [online picture] from http://www.esrl.noaa.gov/gmd/obop/mlo/

Gleick, PH (1993). Water in Crisis: A Guide to the World's Freshwater Resources. Oxford University Press. p. 13, Table 2.1 "Water reserves on the earth"

Zhao L (2013) Evapotranspiration estimation methods in hydrological models. Journal of Geographical Sciences 23:359 -369

Kürschner WM, Wagner F, Visscher EH, Visscher H (1997) Predicting the response of leaf stomatal frequency to a future CO2-enriched atmosphere: Constraints from
historical observations. Geol Rundsch 86:512–517.

IPCC (2007) Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. pp 104

Beerling DJ, Franks PJ (2010) Plant science: The hidden cost of transpiration. Nature 464:495–496.

Kürschner WM, van der Burgh J, Visscher H, Dilcher DL (1996) Oak leaves as biosensors of late neogene and early pleistocenepaleoatmospheric CO2 concentrations. Mar Micropaleontol 27:299–312.

Raven JA (2002) Selection pressures on stomatal evolution. New Phytol 153:371–386

Wagner F, Kouwenberg LLR, van Hoof TB, Visscher H (2004) Reproducibility of Holocene atmospheric CO2 records based on stomatal frequency. Quat Sci Rev 23: 1947–1954.

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. Annu Rev Plant Physiol 33:317–345.

Gedney N (2006) Detection of a direct carbon dioxide effect in continental river runoff records. Nature 439:835–838.

Katul G, Manzoni S, Palmroth S, Oren R (2010) A stomatal optimization theory to describe the effects of atmospheric CO2 on leaf photosynthesis and transpiration. Ann Bot (Lond) 105:431–442.

Lammertsma E, de Boer HJ, Dekker SC, Dilcherc DL, Lotter AF, Wagner-Cremer F. (2011) Global CO2 rise leads to reduced maximum stomatal conductance in Florida vegetation PNAS vol. 108 no. 10 4035-4040

NASA (2013), The water cycle [online afbeelding] van http://earthobservatory.nasa.gov/Features/Water/page2.php

Lindner M, Maroschek M, Netherer S, Kremer A,, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstro¨ma M, Lexer M, Marchetti M (2010) Climate change impacts, adaptive capacity and vulnerability of European forest ecosystems. Forest Ecology and Management 259: 698–709

UIC (2013), Transport in plants [online picture] from http://www.uic.edu/classes/bios/bios100/lectf03am/guardcells01.gif

Wertin TM, McGuire MA, Teskey RO (2012) Effects of predicted future and current atmospheric temperature and [CO2] and high and low soil moisture on gas exchange and growth of Pinus taeda seedlings at cool and warm sites in the species range Tree Physiology 32,: 847–858

Maseyk K, Hemming D, Angert A, Leavitt SW, Yakir D (2011) Increase in water-use efficiency and underlying processes in pine forests across a precipitation gradient in the dry Mediterranean region over the past 30 years Oecologia 167:573–585

Wassen MJ, de Boer HJ, Fleischer K, Rebel KT, Dekker SC (2013) Vegetation-mediated feedback in water, carbon, nitrogen and phosphorus cycles Landscape Ecology 28:599–614

Wikimedia (2013), Natural regeneration Mediterranean forest [online picture] from http://commons.wikimedia.org/wiki/File:Natural_regeneration_Mediterranean_forest.jpg

Huang JG, Bergeron Y, Denneler B, Berninger F, Tardiff J (2007) Response of forest trees to increased atmospheric CO2. Crit Rev Plant Sci 26:265–283