Growth Response of Grassland Species to Elevated CO_2 when Water Stressed

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GROWTH RESPONSE OF GRASSLAND SPECIES TO ELEVATED CO_2 WHEN WATER STRESSED

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As the air's CO_2 content continues to rise, nearly all of earth's plants should exhibit increases in photosynthesis and biomass production; but climate alarmists periodically claim that water stress will negate these benefits. In reviewing the scientific literature of the ten-year period 1983-1994, however, Idso and Idso (1994) concluded that water stress will *not* negate the CO_2-induced stimulation of plant productivity. In fact, they discovered that the CO_2-induced *percentage* increase in plant productivity was nearly always *greater* under water-stressed conditions than it was when plants were well-watered. And seven years later, Poorter and Perez-Soba (2001)[1] conducted a similar literature review and came to the same conclusion. In this summary, therefore, we provide some background for this phenomenon and highlight some of the most impressive work that has subsequently been done in this area.

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At the same time, CO_2-induced increases in root development and CO_2-induced reductions in leaf stomatal conductance often combine to maintain a more favorable plant water status during times of drought. In the case of four grassland species comprising a pasture

[1] http://www.co2science.org/articles/V4/N42/B1.php.
[2] http://www.co2science.org/articles/V2/N24/B1.php.
[3] http://www.co2science.org/articles/V4/N13/B1.php.

characteristic of New Zealand, for example, Clark *et al*. (1999)[4] found that leaf water potential, which is a good indicator of plant water status, was consistently higher (less negative and, therefore, less stressful) under elevated atmospheric CO_2 concentrations. Likewise, leaf water potentials of the water-stressed C_4 grass *Panicum coloratum* grown at 1000 ppm CO_2 were always higher than those of their water-stressed counterparts growing in ambient air (Seneweera *et al*., 2001[5]). In fact, Seneweera *et al*. (1998)[6] had earlier reported that leaf water potentials observed in CO_2-enriched water-stressed plants were an amazing *three-and-a-half times greater* than those observed in control plants grown at 350 ppm during drought conditions (Seneweera *et al*., 1998[7]).

So if atmospheric CO_2 enrichment thus allows grassland plants to maintain an improved water status during times of water stress, it is only logical to expect that such plants will exhibit greater photosynthetic rates than similar plants growing in ambient air. In a severe test of this concept, Ward *et al*. (1999)[8] found that *extreme* water stress caused 93 and 85% reductions in the photosynthetic rates of two CO_2-enriched grassland species; yet their rates of carbon fixation were still greater than those observed under ambient CO_2 conditions.

In view of these several observations, which demonstrate the fact that elevated CO_2 nearly always enhances photosynthetic rates during times of water stress, one would expect that plant biomass production would also be enhanced by elevated CO_2 concentrations under drought conditions. And so it is. On the American prairie, for example, Owensby *et al*. (1999)[9] found that tallgrass ecosystems exposed to twice-ambient concentrations of atmospheric CO_2 for eight years only exhibited significant increases in above- and below-ground biomass during years of less-than-average rainfall. Also, in the study of Derner *et al*. (2001)[10], the authors reported that a 150-ppm increase in the CO_2 content of the air increased shoot biomass in two C_4 grasses by 57%, regardless of soil water content. Moreover, Seneweera *et al*. (2001)[11] reported that a 640-ppm increase in the air's CO_2 content increased shoot dry mass in a C_4 grass by 44 and 70% under well-watered and water-stressed conditions, respectively. Likewise, Volk *et al*. (2000)[12] grew calcareous grassland assemblages at 360 and 600 ppm CO_2 and documented 18 and 40% CO_2-induced increases in whole-community biomass under well-watered and water-stressed conditions, respectively.

Jumping a few years forward in time, Nelson *et al*. (2004)[13] reported on a five-year study (1997-2001) that they had conducted on the semi-arid shortgrass steppe (SGS) of Colorado, USA. Working at the USDA-ARS Central Plains Experimental Range in the northern portion of the SGS about 60 km northeast of Fort Collins, Colorado, they used large (15.5 m^2) open-top chambers to examine the effects of elevated CO_2 (720 vs. 360 ppm) on plant water relations, ecosystem

4 http://www.co2science.org/articles/V2/N9/B2.php.
5 http://www.co2science.org/articles/V4/N37/B1.php.
6 http://www.co2science.org/articles/V2/N6/B2.php.
7 http://www.co2science.org/articles/V2/N6/B2.php.
8 http://www.co2science.org/articles/V3/N16/B2.php.
9 http://www.co2science.org/articles/V2/N14/B2.php.
10 http://www.co2science.org/articles/V4/N30/B3.php.
11 http://www.co2science.org/articles/V4/N37/B1.php.
12 http://www.co2science.org/articles/V4/N13/B1.php.
13 http://www.co2science.org/articles/V7/N25/EDIT.php.

water use efficiency, soil moisture dynamics and root distributions of the ecosystem's dominant C_3 (*Pascopyrum smithii* and *Stipa comata*) and C_4 (*Bouteloua gracilis*) grasses. And what did they find?

The five Agricultural Research Service scientists and their collaborator from Colorado State University report that "seasonal average soil moisture throughout the soil profile (0-15, 15-45, 45-75, 75-105 cm) was increased under elevated CO_2compared to ambient CO_2 for much of the study period," with the greatest relative increase (16.4%) occurring in the 75-105 cm depth increment. They remark that this finding of "increased soil moisture under elevated CO_2 at the deepest soil depth suggests that water percolated deeper into the soil profile and that less moisture was lost to evapotranspiration under elevated CO_2." Noting that "this phenomenon enhances water storage in the deep fine sandy loam soils underlying large portions of the SGS," they went on to say that "this increase in soil moisture has been shown to be the major controlling factor in improved carbon assimilation rates and increased total aboveground biomass in this system (LeCain *et al*., 2003) and will likely decrease the susceptibility of the SGS to drought."

Another important finding of the group of Colorado researchers was, as they describe it, that when averaged over the study period, "leaf water potential was enhanced 24-30% under elevated CO_2 in the major warm- and cool-season grass species of the SGS (*Bouteloua gracilis*, C_4, 28.5%; *Pascopyrum smithii*, C_3, 24.7%; *Stipa comata*, C_3, 30.4%)." And they say these results are similar to those of "studies involving other C_3 and C_4 grass species (Owensby *et al*., 1993; Jackson *et al*., 1994)," and that the enhanced leaf water potential - "which reflects improved plant water status and increased drought tolerance (Tyree and Alexander, 1993)" - may lead to increased leaf turgor and allow the grasses "to continue growth further into periods of drought." Hence, it is not surprising that, averaged over the five years of the study, Nelson *et al*. found that "water-use efficiency (grams aboveground biomass harvested / kilogram water consumed) was 43% higher in elevated than ambient CO_2 plots."

In discussing the *broader* implications of their findings, the scientists say their results "suggest that a future, elevated CO_2 environment may result not only in increased plant productivity due to improved water use efficiency, but also lead

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to increased water drainage and deep soil moisture storage in this semi-arid grassland ecosystem." And they say that "this, along with the ability of the major grass species to maintain a favorable water status under elevated CO_2, should result in the SGS being less susceptible to prolonged periods of drought."

That Nelson *et al*.'s findings are the norm and not the exception is confirmed by their noting that "previous studies have reported increased soil moisture under elevated CO_2 in semi-arid C_3 annual grasslands in California (Fredeen *et al*., 1997), mesic C_3/C_4 perennial tallgrass prairie in Kansas (Owensby *et al*., 1993, 1999; Ham *et al*., 1995; Bremer *et al*., 1996), and mesic C_3 perennial grasslands in Switzerland (Niklaus *et al*., 1998) and Sweden (Sindhoj *et al*., 2000)." Hence, we can validly expect the beneficent effects of atmospheric CO_2 enrichment revealed in this impressive study to be found in grasslands throughout the world as the air's CO_2 content continues to rise to double-and-beyond its current concentration.

But what if air temperature rises concurrently? Actually, things could get even *better* under that scenario. Nelson *et al*. note, for example, that "air temperature was on average 2.6°C higher inside the chambers than outside," and they say that this warming "was implicated in the 36% enhanced biomass production observed in chambered-ambient compared to non-chambered plots." Consequently, since this already-enhanced biomass production was the *starting point* from which the 41% increase in biomass elicited by the doubling of the air's CO_2 content was calculated, the increase in biomass caused by the concurrent actions of *both* factors (increasing air temperature and CO_2 concentration) could well be something on the order of 90%.

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Also publishing in 2004 was the 15-member team of Morgan *et al*. (2004)[14], who - in a review of the scientific literature pertaining to the role of *water relations* in the response of grassland and desert ecosystems to elevated levels of atmospheric CO_2 - wrote that "atmospheric CO_2 enrichment may stimulate plant growth either directly through (1) enhanced photosynthesis or indirectly through (2) reduced plant water consumption and hence slower soil moisture depletion, or the combination of both." And within this context they went on to describe "gas exchange, plant biomass and species responses of five native or semi-native temperate and Mediterranean grasslands and three semi-arid systems to CO_2enrichment, with an emphasis on water relations."

In general terms, the team found that "increasing CO_2 led to decreased leaf conductance for water vapor, improved plant water status, altered seasonal evapotranspiration dynamics, and in most cases, periodic increases in soil water content," such that "across the grasslands of the Kansas tallgrass prairie, Colorado shortgrass steppe and Swiss calcareous grassland, increases in aboveground biomass from CO_2 enrichment were relatively greater in dry years." In contrast, they report that "CO_2-induced aboveground biomass increase in the Texas C_3/C_4 grassland and

[14] http://www.co2science.org/articles/V7/N31/B2.php.

the New Zealand pasture seemed little or only marginally influenced by yearly variation in soil water, while plant growth in the Mojave Desert was stimulated by CO_2 in a relatively wet year." In addition, they say that "Mediterranean grasslands sometimes failed to respond to CO_2-related increased late-season water, whereas semiarid Negev grassland assemblages profited." And although they remark that "vegetative and reproductive responses to CO_2 were highly varied among species and ecosystems, and did not generally follow any predictable pattern in regard to function groups," they say that, considered in their entirety, the literature results they reviewed (many of which they themselves had been instrumental in collecting) "suggest that the indirect effects of CO_2 on plant and soil water relations may contribute substantially to experimentally induced CO_2-effects."

Six years later, Lazzarotto *et al*. (2010)[15] wrote that "white clover (*Trifolium repens* L.) is the most important pasture legume grown in temperate climates in association with a variety of grasses, notably perennial ryegrass (*Lolium perenne* L.)," adding by way of explanation that "white clover improves the nutritional quality and digestibility of the herbage," and that it "contributes substantially to the nitrogen status of the sward through biological nitrogen fixation." They say, however, that there is some concern that future drought, such as is predicted by climate alarmists to occur in tandem with CO_2-induced global warming, will hurt clover more than the grass with which it is intermingled, thereby degrading the nutritional quality and digestibility of pasture swards.

In light of this mix of facts and presumptions, Lazzarotto *et al*. planned and conducted a study wherein, as they describe it, "mechanisms controlling transient responses to elevated CO_2 concentration and climate change in an unfertilized grassland on the Swiss Plateau were examined in light of simulations with PROGRASS," a process-based model of grass-clover interactions developed by Lazzarotto *et al*. (2009), where "daily weather for a series of transient climate scenarios spanning the 21st century were developed for the study site with the help of the LARS-WG weather generator," which is described by Semenov and Barrow (1997) and Semenov *et al*. (1998), and where "changes in the length of dry and wet spells, temperature, precipitation and solar radiation defining the scenarios were obtained from regional climate simulations carried out in the framework of the PRUDENCE project," which is described by Christensen and Christensen (2007).

This work revealed that "compared to 1961-1990," in the words of the Swiss and UK scientists, the climate scenarios they developed for a CO_2 increase from 370 to 860 ppm "indicated that for 2071-2100 there would be a noticeable increase in temperature (roughly 3°C in winter and 5°C in summer), a significant drop in summer precipitation (of the order of -30%) and a nearly 2-fold increase in the length of dry spells." So how strongly were these significant negative changes in climate calculated to affect the grass-clover swards?

The four researchers report that "clover abundance did not decline even in the absence of CO_2 stimulation." And when the atmospheric CO_2 concentration was programmed to gradually rise from an initial value of 370 ppm to a final value of 860 ppm, they found that "clover

[15] http://www.co2science.org/articles/V13/N33/B3.php.

development benefited from the overall positive effects of CO_2 on nitrogen acquisition," which they say was also "the reason for increasing productivity of the [entire] sward."

For Swiss grass-clover swards, therefore, it would appear that the rather large *increases in temperature and decreases in precipitation* that are predicted for the remainder of the 21st century, *even if they come to pass*, will not have much of an effect on them, but that the concomitant increase in the air's CO_2 content will benefit them considerably. In addition, Lazzarotto *et al*. say it is likely that "technical progress in the management of grasslands and pastures," which will surely occur, will help such pastures even more. All things considered, therefore, the future of Switzerland's (and many other countries') clover-grass associations would appear to be bright indeed.

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Last of all, and noting that "grassland communities constitute an important fraction of the green surface of the earth, and are worldwide an important source of cattle-food (Carlier *et al*., 2009; Ciais *et al*., 2011)," Farfan-Vignolo and Asard (2012)[16] investigated several physiological and molecular (antioxidant) responses to water deficit in two major grassland species (*Lolium perenne* L. and *Medicago lupulina* L.) under current *ambient* (A) and future *elevated* (E) atmospheric CO_2 concentrations and air temperatures (T), where $ECO_2 = ACO_2 + 375$ ppm, and where ET = AT + 3°C. In doing so, they found that "drought caused significant increases in oxidative damage, i.e., in protein oxidation and lipid peroxidation levels." But they also found that "in both species the impact of drought on protein oxidation was reduced in future climate conditions [ECO_2 and ET]." And speaking of the stress-reducing effect of ECO_2, they say that "this 'CO_2-protection effect' is reported for a variety of abiotic stress conditions and species," citing the studies of Schwanz and Polle (1998), Sgherri *et al*. (2000), Geissler *et al*. (2009), Perez-Lopez *et al*. (2009), Vurro *et al*. (2009) and Salazar-Parra *et al*. (2012), after which they indicate that they too "find support for this effect at the level of oxidative cell damage and protein oxidation in water-deficit responses of *L. perenne* and *M. lupulina*." And, of course, they also found that *even under drought stress*, "elevated CO_2 significantly affected shoot production in *L. perenne* (increase by 27-32%)," and that "also in *M. lupulina* a biomass increase was observed (26-38%)."

In summary, the conclusions of Idso and Idso (1994), based on the pre-1994 literature, are well supported by the subsequent peer-reviewed scientific literature, which indicates that the

[16] http://www.co2science.org/articles/V16/N6/B1.php.

ongoing rise in the air's CO_2 content will likely lead to substantial increases in plant photosynthetic rates and biomass production, even in the face of stressful environmental conditions imposed by less-than-optimum soil moisture conditions.

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