

BENEFITS OF ATMOSPHERIC CO₂ ENRICHMENT ON SUNFLOWER



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The common sunflower (*Helianthus annuus*) is a large annual forb of the genus *Helianthus*. First domesticated in the Americas, sunflower is cultivated across the world for its oil and fruits. Sunflower seeds (the edible fruit) are typically produced and sold as a snack food for human consumption, bird feed, or as livestock forage. Sunflower oil (extracted from the seeds) is commonly used in cooking, but it is also utilized as a biofuel in the emerging biodiesel market. Additionally, sunflowers are cultivated for the production of latex and nonallergenic rubber.

As one of the top 35 crops in terms of global food production, it is important to understand how this important agricultural species will respond to increases in the air’s CO₂ content. This summary reviews the results of several important studies evaluating the impacts of elevated CO₂ and other growth-related variables on sunflower plants.

Starting first with a study examining *historic* sunflower growth, [Magrin et al. \(2005\)](#)¹ evaluated changes in climate over the 20th century along with changes in the yields of the region’s chief crops, including sunflower, for nine areas of contrasting environment within the Pampas region of Argentina, which accounts for over 90% of the country’s grain production. Then, after determining upward low-frequency trends in yield due to technological improvements in crop genetics and management techniques plus the aerial fertilization effect of the historical increase in the air’s CO₂ concentration, these annual yield anomalies and concomitant climatic anomalies were used to develop relations describing the effects of precipitation, temperature and solar radiation on crop yields, so that the effects of long-term changes in these climatic parameters on Argentina agriculture could be determined.

As one of the top 35 crops in terms of global food production, it is important to understand how this important agricultural species will respond to increases in the air’s CO₂ content. This summary reviews the results of several important studies evaluating the impacts of elevated CO₂ and other growth-related variables on sunflower plants.

Although noting that “technological improvements account for most of the observed changes in crop yields during the second part of the 20th century,” which totaled 102% for sunflower, Magrin *et al.* report that due to changes in climate between the periods 1950-70 and 1970-99, yields increased by 12% in sunflower. Thus, twentieth-century climate change, which is claimed

¹ <http://www.co2science.org/articles/V8/N50/B1.php>

by climate alarmists to have been *unprecedented over the past two millennia* and is often described by them as *one of the greatest threats ever to be faced by humanity*, has definitely *not* been a problem for sunflower growth and yields in Argentina. In fact, it has *helped* it.

Moving on with an eye toward the *future*, [Sims et al. \(1999\)](http://www.co2science.org/articles/V2/N15/B1.php)² grew sunflowers in large controlled-environment chambers receiving ambient and twice-ambient concentrations of atmospheric CO₂ to study the effects of elevated CO₂ on canopy photosynthesis. Results indicated that exposure to twice-ambient atmospheric CO₂ concentrations enhanced rates of net photosynthesis in individual upper-canopy sunflower leaves by approximately 50%.

Sunflowers should become more efficient at absorbing sunlight and using its energy to convert CO₂ into carbohydrates as the air's CO₂ content increases in the future. And, as the efficiencies of these processes increase, net photosynthetic rates and biomass production should also increase, which hypothesis is borne out in several additional works cited below.

[Luo et al. \(2000\)](http://www.co2science.org/articles/V5/N16/B1.php)³ planted and grew sunflowers (cv. Johnny's Albin) in large environmentally-controlled chambers receiving atmospheric CO₂ concentrations of 400 and 750 ppm to determine the effects of elevated CO₂ on canopy light utilization and photosynthetic carbon uptake in this important agronomic crop. They determined that elevated CO₂ increased canopy quantum yield by 32%; and this enhancement of plant light utilization increased canopy carbon uptake by fully 53%.

The above findings suggest that sunflowers should become more efficient at absorbing sunlight and using its energy to convert CO₂ into carbohydrates as the air's CO₂ content increases in the future. And, as the efficiencies of these processes increase, net photosynthetic rates and biomass production should also increase, which hypothesis is borne out in several additional works cited below.

[Zerihun et al. \(2000\)](http://www.co2science.org/articles/V4/N27/B1.php)⁴ grew sunflowers for one month in pots of three different soil nitrogen concentrations that were placed within open-top chambers maintained at atmospheric CO₂ concentrations of 360 and 700 ppm in an attempt to validate predicted

growth responses to atmospheric CO₂ enrichment using a functional balance model they developed. Their work revealed that atmospheric CO₂ enrichment reduced average rates of root nitrogen uptake by about 25%, which reduction would normally tend to reduce tissue nitrogen contents and relative growth rates of seedlings. However, the elevated CO₂ also increased photosynthetic nitrogen-use efficiency by an average of 50%, which increase normally tends to increase the relative growth rates of seedlings. Of these two competing effects, the latter was much more significant, ultimately leading to an increase in whole plant biomass. After just one month, for example, CO₂-enriched plants exhibited whole plant biomass values that were 44, 13

² <http://www.co2science.org/articles/V2/N15/B1.php>

³ <http://www.co2science.org/articles/V5/N16/B1.php>

⁴ <http://www.co2science.org/articles/V4/N27/B1.php>

and 115% greater than those of control plants growing in ambient air at low, medium and high levels of soil nitrogen, respectively. Thus, low tissue nitrogen contents, as predicted by the authors' model and validated by their data, do not necessarily preclude a growth response to atmospheric CO₂ enrichment, particularly if photosynthetic nitrogen-use efficiency is enhanced, which is typically the case with atmospheric CO₂ enrichment.

Getting off to a good start is an important aspect of successful plant development and growth; and elevated CO₂ appears to help sunflower plants considerably in this regard. Noting that "the size and growth rate of a seedling is critical for its competitiveness and survival," [Lehmeier et al. \(2005\)](#)⁵ studied the developmental history of well-watered and fertilized sunflower (cv. Sanluca) plants for the first 15 days after their initial imbibition of water while growing in pots of washed quartz sand in growth chambers maintained at atmospheric CO₂ concentrations of either 200 or 1000 ppm. As soon as the cotyledons started to rapidly expand at 4 DAI (days after imbibition), the expansion rate in the CO₂-enriched air was about 20% faster than that in the CO₂-reduced air; and from that point in time, Lehmeier *et al.* report that "seedling growth was near exponential, with a 2-2.5 times higher rate at elevated CO₂," due largely to an increased unit leaf rate of net carbon assimilation (+120%) and an increased rate of leaf expansion (+60%). By the end of the experiment at 15 DAI, these phenomena had resulted in a 2.5-fold increase in seedling biomass in the CO₂-enriched air compared to the CO₂-reduced air.

Writing as background for their study, [Pal et al. \(2014\)](#)⁶ note that sunflower is one of the world's major oilseed crops, accounting for about 14% of the world's production of seed oil, which they say "is generally considered as premium oil, because of its light color, high level of unsaturated fatty acids, lack of transfat and high oxidative stability," *further* noting that the crop "has potential health benefits because it contains very high concentrations of polyunsaturated fatty acids" -- with more than 90% of them being linoleic and oleic acids -- which they indicate are "considered good for human consumption." As their contribution to determining how sunflower seed oil might be impacted as the air's CO₂ content continues to rise, the six scientists grew two sunflower genotypes -- DRSH 1 (a hybrid) and DRSF 113 (a promising variety) -- under natural field conditions within open-top chambers maintained at either ambient (370 ppm) or enriched (550 ppm) atmospheric CO₂ concentrations. This they did following standard agronomic practices and irrigating when needed to maintain the soil moisture level at field capacity. And what did their study reveal?

Based on the results of the many measurements they made throughout the crop's growth and post-harvest, Pal *et al.* found that (1) the CO₂-induced enhancement in photosynthesis "was 31.7-52.1% in DRSH1 and 25.5-42.8% in DRSF 113," that (2) "plants grown under elevated CO₂ concentration showed 61-68% gains in biomass and 35-46% increases in seed yields of both genotypes," that (3) "oil content increased significantly in DRSF 113 (15%), that (4) "carbohydrate seed reserves increased with similar magnitudes in both the genotypes under elevated CO₂ treatment (13%)," and that (5) "fatty acid composition in seed oil contained higher proportions

⁵ <http://www.co2science.org/articles/V9/N13/B1.php>

⁶ <http://www.co2science.org/articles/V18/feb/a15.php>

of unsaturated fatty acids (oleic and linoleic acid) under elevated CO₂ treatment,” which result they say “is a desirable change in oil quality for human consumption.” Thus, not only was the quantity of seed oil enhanced under elevated CO₂, but the *quality* was as well.

Thus, not only was the quantity of seed oil enhanced under elevated CO₂, but the quality was as well.

Higher levels of atmospheric CO₂ have been shown to provide other ancillary benefits beyond increases in photosynthesis and biomass. One example comes from the work of [Qaderi and Reid \(2011\)](#)⁷, who report that the release of aerobic methane (CH₄) by vegetation has been indirectly confirmed by the field studies of Braga do Carmo *et al.* (2006), Crutzen *et al.* (2006) and Sanhueza and Donoso (2006), as well as by the satellite studies of Frankenberg *et al.* (2005, 2008). In addition, they note that CH₄ emissions from plants can be stimulated by higher air temperatures (Vigano *et al.*, 2008; Qaderi and Reid, 2009) and water stress (Qaderi and Reid, 2009). And since “methane is the second most important long-lived greenhouse gas after carbon dioxide and is thought to be ~25 times more potent than CO₂ in its ability to act as a greenhouse gas,” as they describe it, they decided to see what effect the ongoing rise in the air’s CO₂ content might possibly have on this phenomenon.

Qaderi and Reid “examined the combined effects of temperature, carbon dioxide and watering regime on CH₄ emissions from six commonly cultivated crop species,” one of which was sunflower, in an experiment where “plants were grown from seeds in controlled-environment growth chambers under two temperature regimes (24°C day/20°C night and 30°C day/26°C night), two CO₂ concentrations (380 and 760 ppm) and two watering regimes (well watered and water stressed),” where the “plants were first grown under 24/20°C for one week from sowing, and then placed under experimental conditions for a further week,” after which “plant growth, gas exchange and CH₄ emission rates were determined.”

In discussing their findings, the two researchers report first of all that they found “no detectable CH₄ from [a] control treatment (without plant tissue), indicating that CH₄ from the experimental treatments was emitted only from plant tissues.” Second, they found that the plants grown under higher temperature and water stress emitted more CH₄ than those grown under lower temperature and no water stress. And third, they found that “elevated CO₂ had the opposite effect,” so that it “partially reverses” the effects of the other two factors. In light of such, Qaderi and Reid conclude that “although rising atmospheric CO₂ reduces plant CH₄ emissions, it may not fully reverse the effects of temperature and drought,” which they assume will increase in tandem with the ongoing rise in the air’s CO₂ content. Nevertheless, this result is still a positive finding. In addition, it may well be *much* more positive than they make it out to be, especially if temperatures and drought do *not* increase with the passage of time and continued increases in the air’s CO₂ content, which many believe to be a real possibility, in that (1) droughts have not been shown to be more prevalent worldwide in warmer as opposed to colder periods of Earth’s history (see [Drought](#) in our Subject Index), and (2) due to the natural oscillatory behavior of Earth’s surface air temperature on millennial timescales -- which over the past two millennia has

⁷ <http://www.co2science.org/articles/V14/N22/B2.php>

successively brought us the last phase of the Roman Warm Period, the Dark Ages Cold Period, the Medieval Warm Period, the Little Ice Age, and the initial phase of the Current Warm Period - it will likely not warm much more than it has already warmed before the globe's mean surface air temperature plateaus out and ultimately begins a slow decline to a cooler state, aided by the ever-increasing CO₂-induced reduction in aerobic plant CH₄ emissions.

Focusing on another aspect of sunflower growth, [Rinaudo et al. \(2010\)](#)⁸ introduce their study by noting that “previous work has emphasized that AMF [arbuscular mycorrhizal fungi] are important for the sustainability of agricultural ecosystems by enhancing crop nutrition (Plenchette et al., 1983; Gosling et al., 2006), by reducing nutrient leaching losses after heavy rain (van der Heijden, 2010), by providing protection against stress and disease (Auge, 2001; Sikes et al., 2009) and by improving soil structure (Rillig and Mummey, 2006). As their contribution to the topic, they explored another positive impact of AMF: their ability to suppress the negative consequences of aggressive agricultural weeds, which each year reduce crop yields around the world by between 10 and 30% (Oerke and Dehne, 1997). More specifically, the team of four researchers set out to investigate “the impact of AMF and AMF diversity (three versus one AMF taxon) on weed growth in experimental microcosms where a crop (sunflower) was grown together with six widespread weed species.”

Rinaudo et al. report their research efforts revealed that “the total biomass of sunflower grown alone in monocultures was 22% higher compared to microcosms where sunflower was grown in mixture together with weeds,” while “the total weed biomass in microcosms with sunflower was on average 47% lower in microcosms with AMF, compared to microcosms without AMF.” And when the weeds were grown alone, the effect of AMF presence was to reduce weed biomass by 25%.

In considering their findings, Rinaudo et al. say their study shows that “AMF have the ability to suppress growth of some aggressive agricultural weeds, including *Chenopodium album* and *Echinochloa crus-galli*, which belong to the top ten of the world's most aggressive weeds.” In addition, they note that the sunflower plants they grew “benefited from AMF through improved phosphorus uptake,” which “points to a novel characteristic of the mycorrhizal symbiosis, namely that AMF have the ability to suppress unwanted weed species, while at the same time promoting nutrition of the target crop species,” which work “supports two earlier reports by Vatovec et al. (2005) and Jordan and Huerd (2008).” And in further commenting on this aspect of their work, they write that “sunflower obtained 48% more phosphorus when AMF were present, while AMF reduced weed phosphorus content of the three mycorrhizal weeds (*Digitaria sanguinalis*, *Echinochloa crus-galli*, *Setaria viridis*) by 21%.”

The significance of the above findings with respect to the ongoing rise in the air's CO₂ content is linked to the relationship that exists between atmospheric CO₂ enrichment and AMF growth and development. As may be seen by perusing the materials identified when searching for *arbuscular mycorrhizal fungi* on our website's [search feature](#)⁹ (home page upper right-hand corner), as the air's CO₂ content rises, it will likely impact crop-fungal interactions by increasing the percent of

⁸ <http://www.co2science.org/articles/V13/N47/B3.php>

⁹ <http://www.co2science.org/cSearch.php>

the crop's root system colonized by either mycorrhizal fungal hyphae or arbuscular structures, thereby promoting the positive phenomena documented by Rinaudo *et al.*

Finally, we highlight one additional benefit rising CO₂ posits for sunflowers. "Phytoextraction," in the words of [Tang *et al.* \(2003\)](#)¹⁰, "has been defined as the direct use of living green plants in order to extract pollutants from contaminated soils and concentrate them into roots and easily harvestable shoots (Baker and Brooks, 1989; Raskin *et al.*, 1994; Salt *et al.*, 1995; Cunningham and David, 1996)." This technique, according to Tang *et al.*, "offers a cost-effective and environmentally sound pollution-remediation option," but that "one of the key problems is how to enhance the uptake of metals by plants in order to increase absolute phytoremediation efficiency." Hence, they decided to see what elevated CO₂ could do in this regard.

To accomplish their objective, Tang *et al.* grew individual sunflower plants from seed in pots with 1 kg natural topsoil laced with different concentrations of copper (Cu) for 24 days in ambient air of 350 ppm CO₂, after which one-third of the plants were exposed to air of 800 ppm CO₂ and another third to air of 1200 ppm CO₂, which elevated concentrations were only supplied between the hours of 8 and 11 a.m. for 12 additional days. At the end of this period, the plants were harvested and the concentrations of copper in their leaves, stems and roots were measured, after which *bioaccumulation factors* (BFs) were calculated as the ratios of average copper concentrations in leaves to the copper concentration in the soil.

In presenting their findings, the authors report that "sunflower grew higher and larger, and had more and thicker leaves, and produced larger leaf areas, compared to the plants growing under ambient CO₂ levels." In addition, the ratio of the observed BF at 800 ppm CO₂ to that observed at 350 ppm CO₂ was 3.4 in natural soil, 10.9 in soil containing 100 mg Cu per kg soil, and 4.2 in soil containing 200 mg Cu per kg soil, while the similar ratios of observed BFs at 1200 ppm CO₂ to that observed at 350 ppm CO₂ were 1.2, 3.8 and 2.6, respectively. Such findings, in the words of Tang *et al.*, are significant "since the increase of plant biomass resulting from CO₂ application could suggest that more metal be taken up from the contaminated growth media, and that the tolerance to metal toxicity be improved," and they add that "obviously, this could help metal

*Such findings, in the words of Tang *et al.*, are significant "since the increase of plant biomass resulting from CO₂ application could suggest that more metal be taken up from the contaminated growth media, and that the tolerance to metal toxicity be improved," and they add that "obviously, this could help metal accumulators survive on the metal stress conditions, shorten the time needed for clean-up of contaminated sites, and, therefore, increase relative phytoremediation efficiency."*

¹⁰ <http://www.co2science.org/articles/V7/N2/B3.php>

accumulators survive on the metal stress conditions, shorten the time needed for clean-up of contaminated sites, and, therefore, increase relative phytoremediation efficiency.” They also note that the large increase in uptake of copper by sunflower, and the alleviation of chlorosis in their leaves with elevated CO₂, suggest sunflower plants “may be able to increase the internal recycling of deficient nutrients resulting from copper stress.” Hence, they conclude that “the use of CO₂ fertilizer for triggering hyperaccumulation in plants, and increasing biomass production, could open up the way for enhanced phytoremediation and for phytomining.”

In summary, it is clear that as the CO₂ content of the air increases, sunflower plants will exhibit physiological adjustments in root nitrogen uptake rates and photosynthetic nitrogen-use efficiency that will ultimately lead to greater amounts of net carbon uptake and biomass production, even on soils severely depleted in nitrogen. Rising CO₂ will also likely reduce sunflower plant CH₄ emissions, increase the ability of sunflowers to withstand negative growth impacts of weeds and enhance their tolerance to heavy metal toxicity. Thus, commercial growers of sunflower crops will likely experience enhanced yields as the atmospheric CO₂ content continues to rise.

For more information on sunflower growth responses to atmospheric CO₂ enrichment see Plant Growth Data: Sunflower ([dry weight](#)¹¹, [photosynthesis](#)¹²).

REFERENCES

- Auge, R.M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* **11**: 3-42.
- Baker, A.J.M. and Brooks, R.R. 1989. Terrestrial higher plants which hyperaccumulate metallic elements - a review of their distribution, ecology, and phytochemistry. *Biorecovery* **1**: 81-126.
- Braga do Carmo, J., Keller, M., Dezincourt Dias, J., Barbosa de Camargo, P. and Crill, P. 2006. A source of methane from upland forests in the Brazilian Amazon. *Geophysical Research Letters* **33**: 10.1029/2005GL025436.
- Crutzen, P.J., Sanhueza, E. and Brenninkmeijer, C.A.M. 2006. Methane production from mixed tropical savanna and forest vegetation in Venezuela. *Atmospheric Chemistry and Physics Discussions* **6**: 3093-0397.
- Cunningham, S.D. and David, W.O. 1996. Promises and prospects of phytoremediation. *Plant Physiology* **110**: 715-719.
- Frankenberg, C., Meirink, J.F., van Weele, M., Platt, U. and Wagner, T. 2005. Assessing methane emissions from global space-borne observations. *Science* **308**: 1010-1014.

¹¹ http://www.co2science.org/data/plant_growth/dry/h/helianthusa.php

¹² http://www.co2science.org/data/plant_growth/photo/h/helianthusa.php

- Frankenberg, C., Bergamaschi, P., Butz, A., Houweling, S., Meirink, J.F., Notholt, J., Petersen, A.K., Schrijver, H., Warneke, T. and Aben, I. 2008. Tropical methane emissions: a revised view from SCIAMACHY onboard ENVISAT. *Geophysical Research Letters* **35**: 10.1029/go08GL034300.
- Gosling, P., Hodge, A., Goodlass, G. and Bending, G.C. 2006. Arbuscular mycorrhizal fungi and organic farming. *Agriculture, Ecosystems and Environment* **113**: 17-35.
- Jordan, N. and Huerd, S. 2008. Effects of soil fungi on weed communities in a corn-soybean rotation. *Renewable Agriculture and Food Systems* **23**: 108-117.
- Lehmeier, C.A., Schauffele, R. and Schnyder, H. 2005. Allocation of reserve-derived and currently assimilated carbon and nitrogen in seedlings of *Helianthus annuus* under subambient and elevated CO₂ growth conditions. *New Phytologist* **168**: 613-621.
- Luo, Y., Hui, D., Cheng, W., Coleman, J.S., Johnson, D.W. and Sims, D.A. 2000. Canopy quantum yield in a mesocosm study. *Agricultural and Forest Meteorology* **100**: 35-48.
- Magrin, G.O., Travasso, M.I. and Rodriguez, G.R. 2005. Changes in climate and crop production during the 20th century in Argentina. *Climatic Change* **72**: 229-249.
- Oerke, E.C. and Dehne, H.W. 1997. Global crop production and the efficacy of crop protection -- current situation and future trends. *European Journal of Plant Pathology* **103**: 203-215.
- Pal, M., Chaturvedi, A.K., Pandey, S.K., Bahuguna, R.N., Khetarpal, S. and Anand, A. 2014. Rising atmospheric CO₂ may affect oil quality and seed yield of sunflower (*Helianthus annuus* L.). *Acta Physiologiae Plantarum* **36**: 2853-2861.
- Plenchette, C., Fortin, J.A. and Furlan, V. 1983. Growth responses of several plant species to mycorrhizae in a soil of moderate P-fertility. 1. Mycorrhizal dependency under field conditions. *Plant and Soil* **70**: 199-209.
- Qaderi, M.M. and Reid, D.M. 2009. Methane emissions from six crop species exposed to three components of global climate change: temperature, ultraviolet-B radiation and water stress. *Physiologia Plantarum* **137**: 139-147.
- Qaderi, M.M. and Reid, D.M. 2011. Stressed crops emit more methane despite the mitigating effects of elevated carbon dioxide. *Functional Plant Biology* **38**: 97-105.
- Raskin, I., Kumar, P.B.A.N., Dushendov, S. and Salt, D.E. 1994. Bioconcentration of heavy metals by plants. *Current Opinions in Biotechnology* **5**: 285-290.
- Rillig, M.C. and Mummey, D.L. 2006. Mycorrhizas and soil structure. *New Phytologist* **171**: 41-53.
- Rinaudo, V., Barberi, P., Giovannetti, M. and van der Heijden, M.G.A. 2010. Mycorrhizal fungi suppress aggressive agricultural weeds. *Plant and Soil* **333**: 7-20.

Salt, D.E., Blaylock, M., Kumar, N.P.B.A., Dushenkov, V., Ensley, B.D., Chet, I. and Raskin, I. 1995. Phytoremediation: A novel strategy for the removal of toxic metals from the environment using plants. *Biotechnology* **13**: 468-474.

Sanhueza, E. and Donoso, L. 2006. Methane emission from tropical savanna *Trachypogon* sp. grasses. *Atmospheric Chemistry and Physics* **6**: 5315-5319.

Sikes, B.A., Kottenie, K. and Klironomos, J.N. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* **97**: 1274-1280.

Sims, D.A., Cheng, W., Luo, Y. and Seeman, J.R. 1999. Photosynthetic acclimation to elevated CO₂ in a sunflower canopy. *Journal of Experimental Botany* **50**: 645-653.

Tang, S., Xi, L., Zheng, J. and Li, H. 2003. Response to elevated CO₂ of Indian mustard and sunflower growing on copper contaminated soil. *Bulletin of Environmental Contamination and Toxicology* **71**: 988-997.

van der Heijden, M.G.,A. 2010. Mycorrhizal fungi reduce nutrient loss from model grassland ecosystems. *Ecology* **91**: 1163-1171.

Vatovec, C., Jordan, N. and Huerd, S. 2005. Responsiveness of certain agronomic weed species to arbuscular mycorrhizal fungi. *Renewable Agriculture and Food Systems* **20**: 181-189.

Vigano, I., van Weelden, H., Holzinger, R., Keppler, F. and Rockmann, T. 2008. Effect of UV radiation and temperature on the emission of methane from plant biomass and structural components. *Biogeosciences Discussions* **5**: 243-270.

Zerihun, A., Gutschick, V.P. and BassiriRad, H. 2000. Compensatory roles of nitrogen uptake and photosynthetic N-use efficiency in determining plant growth response to elevated CO₂: Evaluation using a functional balance model. *Annals of Botany* **86**: 723-730.

