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C₃ AND C₄ PLANTS

What Are the Differences?

 C_3 and C_4 are two of the three different processes (see <u>video</u>) that plants use to fix carbon (C) during photosynthesis (PS). This C-fixing is the way plants remove C from atmospheric carbon dioxide (CO₂) to create organic molecules such as carbohydrates.

A C_3 plant uses a pathway that produces a 3-carbon molecule called 3-phosphoglyceric acid. About 85% of the earth's plants use this C_3 pathway to fix C via the Calvin cycle. During this one-step process, the enzyme RuBisCo (ribulose-1,5-biphosphate carboxylase/oxygenase) causes an oxidation reaction in which some of the energy used in PS is lost through **photorespiration (PR)**, and this results in about a 25% reduction in the amount of C that is fixed by the plant. This lost C is released back to the atmosphere as CO_2 . Soybeans, cotton, wheat, and rice are common C_3 crop plants.

In C₄ plants, the light-dependent reactions and the Calvin Cycle are physically separated. The light-dependent reactions occur in the mesophyll cells (spongy tissue in the middle of the leaf), and the Calvin Cycle occurs in bundle-sheath cells (cells around the leaf veins) (this cellular structure is known as Kranz anatomy). A C₄ plant produces the intermediate 4-carbon molecules malic or aspartic acid during the carbon-fixing process. This intermediate step in the pathway before the Calvin Cycle reduces the amount of C that is lost to the atmosphere in the overall process.

The CO_2 that is taken in by a C_4 plant is moved to the bundle sheath cells (also contain chloroplasts) by the malic or aspartic acid molecules (now called malate and aspartate molecules). The oxygen (O) content in the bundle sheath cells is very low, so the RuBisCo enzymes are less likely to catalyze oxidation reactions and waste C molecules. The malate and aspartate molecules release the CO_2 in the chloroplasts of the bundle sheath cells and the Calvin Cycle begins. C_4 crop plants include corn, sugar cane, sorghum, and switchgrass.

The **PR** that occurs in C_3 plants when the Calvin Cycle enzyme RuBisCo acts on O rather than CO_2 is wasteful, and C_3 plants have no feature to reduce or eliminate PR. C_4 plants minimize PR by separating initial CO_2 fixation and the Calvin Cycle in the different cell types described above. Photorespiration uses up fixed C, wastes energy, and tends to happen when plants close their stomata to reduce water loss. High temperatures make it worse.

Water Use Efficiency (WUE)

An article titled "Quantifying water and CO₂ fluxes and water use efficiencies across irrigated C₃ and C₄ crops in a humid climate" by Anapalli et al. paints an interesting picture of how choice of crop either in monoculture or in a rotation can influence WUE of irrigated crops.

Abbreviations used in the article are as follows:

- *EWUE*–crop-ecosystem water use efficiency, or the amount of CO₂ removed from the soil-crop-air system per unit of water used in ET.
- ET-evapotranspiration.
- NEE-net ecosystem exchange, measured in lb. CO₂
 per acre; represents the balance from the amount of
 CO₂ fixed in photosynthesis minus the CO₂ released
 in plant respiration and as a byproduct of organic
 matter decomposition in the soil; expressed as a
 negative value if the net flux of CO₂ is coming down
 toward the crop or sink.
- WUE-net carbon gain from photosynthesis to water lost through transpiration at the leaf level. In agricultural science, WUE is used to denote the ratio of the amount of harvested yield, either grain or biomass, to the amount of water used in producing that yield.
- EC-eddy covariance-provides quantification of EWUE at the crop-ecosystem level by measuring the CO₂ and water fluxes between the atmosphere and land surface. This is achieved by measuring the covariance of the vertical wind speed for eddy transport and the concentrations of CO₂ and water vapor in the eddies.
- The objectives of the study were to quantify 1) NEE and ET from C₄ (corn) and C₃ (soybean and cotton) cropping systems in the lower Miss. Delta, and 2) EWUE across these three cropping systems for irrigation water management applications.
- The research reported in this article was conducted at Stoneville, Miss., which has a sub-tropical humid climate with mild winters and warm summers. Dominant soil series in all crop fields is Tunica clay.
- Corn was planted in 38-in.-wide rows on Mar. 21, 2017, was fully emerged on Mar. 28, and reached physiological maturity (PM) on July 17, or 111 days after emergence (DAE).
- Soybean was planted in 30-in.-wide rows on Apr. 21, 2017, was fully emerged on Apr. 28, and reached PM on Sept. 10, or 135 DAE.
- Cotton was planted in 30-in.-wide rows on Apr. 22, 2017, was fully emerged on May 1, and reached PM on



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Sept. 10, or 132 DAE.

- All study sites were irrigated by the furrow method to maintain soil water content in the upper 12 in. of soil at >65% plant available water.
- Eddy covariance methodology was used to measure CO₂ and water fluxes between the atmosphere and land surface in all fields (click here for an article with details about the setup and use of a network of towers throughout the Delta to quantify carbon and water fluxes in the Lower Miss. River Basin).
- In general, there were only minor differences in the air temperatures above the canopies of the three crops.
- Compared to soybean and cotton, soil temperatures under corn remained cooler throughout the growing season.
 Soil temperatures under cotton were the hottest and soil temperatures under soybean were intermediate to those under corn and cotton. This was likely related to earlyseason corn leaf area index (LAI) being the greatest and cotton LAI being the lowest. The LAI of crop plants in a cropping system has the most influence on NEE.
- All three crops were a net sink for CO₂: corn, soybean, and cotton fixed -31,331, -23,563, and -8,856 kg CO₂ per ha in exchange for 483, 552, and 367 mm of ET, respectively (negative values for fixed CO₂ show that CO₂ fixed in the plant is removed from the atmosphere).
- Corn grain yield averaged 203.7 bu/acre, soybean seed yield averaged 71.1 bu/acre, and cotton lint yield averaged 1124 lb/acre.
- Daily biomass accumulation was highest in corn, followed by soybean, and least in cotton.
- Highest NEE was in corn, followed by soybean followed by cotton. Seasonal NEE estimated for cotton was 72% less than that for corn and 62% less than that for soybean. Thus, corn, the C₄ crop, fixed more CO₂ for a given amount of resources than did the C₃ crops soybean and cotton.
- Maximum ET from corn, soybean, and cotton was 0.252, 0.26, and 0.224 in./day, respectively. Whole season ET for corn, soybean, and cotton was 19.0, 21.7, and 14.5 in., respectively. The lower cotton ET was due to its lower LAI compared to soybean and corn.
- Half-hour estimates of ET from all crops were most correlated with solar radiation ($R^2 = 0.77$) vs. air temperature ($R^2 = 0.34$) and vapor pressure deficit ($R^2 = 0.53$) in this study that was conducted in the sub-humid climate of the Delta.
- Overall, daily EWUE in all three crops followed the LAI growth patterns. Higher rates of EWUE were achieved in all three crops during the peak LAI stages of those crops.
- The EWUE in corn (53 kg CO₂/ha per mm of ET) was greater than that of soybean (43 kg CO₂/ha per mm of

- ET) which was greater than that of cotton (24 kg CO₂/ha per mm of ET).
- The corn crop's grain production WUE (expressed as the ratio of the grain weight to the amount of ET) was 26 kg/ha per mm of ET. The WUE of soybean seed production was 9 kg/ha per mm of ET, and that of cotton lint yield was 3 kg/ha per mm of water.
- The authors conclude that the results from this study can be used to make decisions about the proper crop mix to use in the Miss. Delta to achieve increased WUE while also sequestering more CO₂ in cropping systems. These results also indicate that C₄ corn is a more efficient user of water than are C₃ soybean and cotton crops.

Producers in the Midsouth who irrigate using water from the declining MRVAA should take note of how selection of a rotation partner with soybeans can affect the amount of product that is produced with a unit of water, and the efficiency of that production. Remember that rice, wheat, and cotton are C_3 crop plants, whereas corn and sorghum are C_4 crop plants.

Ozone (O₃) effects on C₃ and C₄ Crops

Ozone is an increasingly important air pollutant, so understanding how an elevated atmospheric O₃ level might affect crop productivity is necessary. An article titled "Similar photosynthesis but different yield responses of C₃ and C₄ crops to elevated O₃" by Shuai et al. provides results from experiments that were conducted to 1) examine the extent of leaf trait variation in C₃ and C₄ crops, 2) analyze how elevated O₃ affects performance of C₃ and C₄ crops, and 3) explore whether or not inbred and hybrid lines of rice and corn show a similar response to O₃. Pertinent points from that article follow.

- The authors used results/data from both published and unpublished studies that spanned the 2002-2021 period.
- Data from five C₃ (included soybean, rice, and wheat)
 and four C₄ (included corn, sorghum, and switchgrass)
 species were used. The crops used represent those
 grown for food and bioenergy production throughout the
 world.
- All crops were grown in both ambient and elevated O₃ environments.
- Results from this meta-analysis quantitatively show that
 O₃ pollution more negatively/severely affects function
 and productivity of C₃ crop plants. That is, C₃ crops are
 more sensitive to elevated O₃ than C₄ crops.
- These results can be used to 1) guide producers in selecting crops that will be more productive where elevated O₃ now exists or will exist, and 2) guide future efforts to improve tolerance of crop plants to elevated O₃ levels.



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The above information should not be misconstrued to mean that C₃ crops should be tossed out in favor of C₄ crops, but it does suggest the logical question of "Why not work at changing major C₃ crop plants to C₄ plants?" so that WUE and O₃ tolerance of all crops can be increased. That does seem logical on the surface. However, according to a statement in the article titled "Integrating C₄ photosynthesis into C3 crops to increase yield potential" by Covshoff and Hibberd, "Owing to complex changes associated with C₄ photosynthesis, it is no understatement to define this conversion as one of the Grand Challenges for Biology in the 21st Century." They "outline the challenges of installing a C4 system and assess how new approaches and knowledge may help achieve this goal." And of course, this task will require sophisticated and complex genetic engineering techniques and methodology. But this endeavor just might be worth the effort when the economic and societal benefits are taken into account; i.e., a reduction in wasteful PR by C₃ plants that might be converted to C₄ plants could result in a significant increase in useable yield from these plants, and the conversion of C₃ to C₄ plants could result in all crop species being more tolerant to O₃ pollution. (Caveat: Since the above article was published 9 years ago, it is likely that numerous strides have been made in reaching this goal.)

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