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Impacts of Climate Change on Stomatal Density and Photosynthetic Efficiency in C3 and C4 Plant Species

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Abstract:
Stomata are small pores in the epidermis which control the balance between uptake of carbon dioxide for photosynthesis and loss of water by transpiration. Climate change upsets this balance, resulting in higher atmospheric CO2, air temperature, vapour-pressure deficit, drought severity and frequency of compound heat-drought events. This review explores the effects of these drivers on the stomatal density and photosynthetic efficiency of plant species belonging to the C3 and C4 categories. Increased CO2 levels are often associated with reduced stomatal conductance and potentially reduced stomatal density based on the available evidence. However, the developmental response depends on species, genotype and environment. The increase of CO2 levels often results in an increase of CO2 absorption through the suppression of photorespiration in C3 plants. However, acclimatisation, nitrogen limitation, stomatal closure and heat stress can all limit realised gains. Direct CO2 fertilisation of photosynthesis is often limited by the CO2-concentrating mechanism in C4 plants. Lower stomatal conductance can improve water status during droughts but also increase the risk of reduced evaporative cooling during heat waves. The effects of stomatal density are influenced by several factors, including stomatal size, kinetics, mesophyll conductance, leaf hydraulics and the timing of stress. So, there's no easy metric for photosynthetic efficiency in stomatal density. Breeding and phenotyping strategies should target dynamic stomatal behaviour, combined anatomical-functional characteristics, and pathway-specific climatic responses, not only density.

Keywords: Climate Change; Stomatal Density; Photosynthetic Efficiency; C3 Plants; C4 Plants; Elevated CO2; Drought; Water-Use Efficiency

Introduction

Climate change is changing the physiological environment in which crops and wild plants take up carbon. Increasing CO2, increasing air temperature, changes in rainfall and more frequent drought and heat events simultaneously influence the biochemical machinery of photosynthesis and the development of stomata. This response is driven by stomata which control the diffusion pathway for CO2 into leaves and water vapour out of leaves. Stomatal density, stomatal size and stomatal aperture changes affect maximum conductance, transpiration, leaf temperature and intrinsic water-use efficiency (Franks & Beerling, 2009; Hetherington & Woodward, 2003; Lawson & Blatt, 2014). However, the same anatomical adjustment may

have different consequences in C3 and C4 species as the two pathways differ in their dependence on intercellular CO2 and their sensitivity to photorespiration and heat (Ghannoum, 2009; Sage and Kubien, 2007).

Stomatal density is often regarded as an adaptive trait in a changing climate. Early evidence from herbarium and chamber studies indicated that stomatal numbers decrease with increasing atmospheric CO2 (Woodward, 1987). Additional work has shown that elevated CO2 also acts through stomatal signalling, mature-leaf to young-leaf communication and guard-cell-linked developmental pathways (Grey et al., 2000; Lake et al., 2001; Xu et al., 2016). However, modern syntheses show that density responses are non-universal. Stomatal density can be reduced, increased or unchanged under elevated CO2 depending on species, leaf surface, light, water status and genotype (Ainsworth & Rogers, 2007; Casson & Grey, 2008; Liang et al., 2023). Thus, the climate sensitivity of stomatal density needs to be interpreted with conductance, kinetics, photosynthetic rate and water relations.

Review scope and analytical framework

This paper adopts a narrative review approach based on peer-reviewed studies that connect climate-change drivers to stomatal traits and photosynthetic performance. The review highlights free-air CO2 enrichment syntheses, stomatal-development studies, C3-C4 comparative physiology, and recent work on compound heat and drought. The aim is to develop mechanisms that can explain that stomatal density can be positively associated with photosynthetic efficiency sometimes and negatively sometimes, not to estimate a single universal effect size. This is important because although stomatal density is easily phenotyped microscopically, the physiological consequences of that density depend on conductance, pore geometry, leaf age and the stress regime under which leaves developed.

The analysis is based on three assumptions. First, while stomatal density is a developmental trait determined primarily during leaf expansion, stomatal aperture is a reversible physiological response. Second, photosynthetic efficiency is broadly defined as the ability to acquire carbon per unit limiting resource, especially water, nitrogen and thermal tolerance. Third, we treat C3 and C4 pathways separately because they have different biochemical limitations. In C3 plants, Rubisco carboxylation competes with oxygenation, so high CO2 can directly increase assimilation and decrease photorespiration. In C4 plants the bundle-sheath CO2 concentrating mechanism already raises CO2 around Rubisco, so that climate effects are more strongly mediated through water status, stomatal conductance and temperature balance (Ghannoum, 2009; Sage & Kubien, 2007).

Stomatal density as a developmental and functional trait

The stomatal density is the number of stomata per unit area of leaf. The stomatal index is the proportion of epidermal cells that differentiate into stomata. Either the plants are changing the timing of stomata initiation or the size of epidermal cells or both, which results in changes in density. This is an important distinction, a decrease in density might be caused by larger epidermal cells rather than less commitment to stomatal lineage. Stomatal development is associated with environmental cues and genes and peptide signals regulating epidermal patterning such as the HIC and EPF-related pathways (Doheny-Adams et al., 2012; Grey et al., 2000; Song et al., 2023). Manipulating stomatal density has the potential to alter plant growth and performance under restricted-water conditions, but the benefit is environment-dependent and requires coordination between density, stomatal size and opening speed (Franks et al., 2015; Lawson & Vialet-Chabrand, 2019).

Only in combination with pore size and aperture is density relevant to the gas-exchange point of view for potential conductance. High stomatal density with small stomata may promote high maximum conductance and fast response to changing light, but may also increase potential water loss if closure is delayed (Franks & Beerling, 2009; Sakoda et al., 2020). Reduction of transpiration at low density may improve water use efficiency, but limit CO2 supply and evaporative cooling under heat stress. This indicates that photosynthetic efficiency under climate change does not optimise only by maximising or minimising stomatal density. It is optimised by matching developmental anatomy to the temporal pattern of environmental stress, canopy light fluctuations, soil water supply and the photosynthetic pathway.

Another complication is that density formed under one set of conditions may work under another set of conditions. Leaves formed in the presence of early season water availability may undergo drought later in the reproductive stage. Likewise, high CO2 during leaf development may reduce the requirement for high stomatal density, but subsequent heat waves may require higher conductance to enable evaporative cooling. Such uncoupling of developmental history from functional demand provides a rationale for the low predictive power of static stomatal density for yield. Therefore, a full assessment of the relative importance of developmental plasticity, controlling the number and architecture of stomata, versus operational plasticity, controlling the rate of pore opening and closing in response to changing light, humidity and water supply (Engineer et al., 2016; Lawson & Blatt, 2014).

Elevated CO2 and stomatal responses

Two major effects of increased CO2 on stomata are rapid decrease in stomatal aperture and in some species a developmental decrease in stomatal density or index. FACE experiments have shown that elevated CO2 generally reduces stomatal conductance but increases carbon gain in many C3 plants (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007). This is physiologically advantageous because at current atmospheric concentrations C3 photosynthesis is generally CO2 limited and photorespiration declines with increasing CO2 relative to O2. This means that partial stomatal closure can enable a C3 leaf to sustain assimilation and even increase assimilation, thus achieving a higher intrinsic water-use efficiency (Leakey et al., 2009; Long et al., 2006).

C4 species are different. In C4 photosynthesis, the direct stimulation of photosynthesis by elevated CO2 is generally of smaller magnitude than in C3 species, due to the high CO2 concentration around Rubisco. However, high CO2 could still have an indirect effect on C4 performance through reduction of stomatal conductance, conserving soil water, improving plant water status and extending photosynthesis during drought (Ghannoum, 2009; Leakey et al., 2009). Studies that compare native and invasive C3 and C4 grasses indicate that CO2 responses depend on species identity and ecological strategy, not pathway (Hager et al., 2016). This suggests that C4 crops may benefit most from elevated CO2 under water-limited conditions whereas well-watered C4 photosynthesis may benefit little.

Responses at the leaf level also interact with leaf area and phenology at the canopy scale. If elevated CO2 decreases conductance but increases leaf area, then total canopy water use may not be reduced as much as predicted from measurements on single leaves. Alternatively, stomatal closure could help to conserve soil moisture so that plants can sustain green leaf area for longer during terminal drought and thus indirectly increase seasonal carbon gain. Hence, FACE studies caution against extrapolation of leaf photosynthesis to yield. The CO2 fertilisation effect in C3 crops might be real but smaller in the field than in enclosure studies, while C4 responses may be principally mediated by improved water relations rather than direct biochemical stimulation (Ainsworth & Long, 2005; Leakey et al., 2009; Long et al., 2006).

Climate driver	Main stomatal-density response	C3 photosynthetic implication	C4 photosynthetic implication
Elevated CO2	Often lowers stomatal conductance and may reduce density/index, but response is genotype- and environment-dependent	Can increase assimilation and iWUE by suppressing photorespiration; acclimation and nitrogen limits may reduce gains	Usually smaller direct CO2 stimulation; lower conductance can conserve soil water under drought
High temperature	Developmental responses vary; heat can interact with VPD and leaf water status	May intensify photorespiration and thermal inhibition, especially above optimum	Often favoured at warm temperatures, but heat waves can impair enzymes and cooling if conductance is low
Drought / low soil water	Can alter stomatal development and reduce conductance; density may increase or decrease by species	Closure restricts CO2 diffusion and reduces A; water saving may protect survival	Water-saving benefits can be strong, but severe drought reduces C4 assimilation and pathway advantage
High VPD / compound heat-drought	Promotes closure and selection for coordinated density, size, and kinetics	Improves water conservation but may reduce carbon gain and canopy cooling	Lower gs may conserve water but increase leaf temperature and heat damage risk

Table 1: Expected stomatal and photosynthetic responses of C3 and C4 plants to major climate-change drivers

Note. A = net CO2 assimilation; gs = stomatal conductance; iWUE = intrinsic water-use efficiency.

Warming, drought, and compound stress

Temperature Effects on Stomata: Metabolism and Water Relations Moderate warming is expected to increase rates of photosynthesis to a thermal optimum but high temperature reduces enzyme stability, increases evaporative demand and can cause stomatal closure if hydraulic stress develops. C3 plants are often more susceptible to high temperature photorespiration since the rate of oxygenation by Rubisco increases with temperature, whereas C4 plants generally have higher photosynthetic efficiency at higher temperatures (Sage & Kubien, 2007). The advantage of C4 is not infinite, however. In C4 leaves, water stress quickly causes a decline in stomatal conductance and CO2 assimilation, and drought diminishes the water-use and nitrogen-use benefits typically linked to C4 photosynthesis (Ghannoum, 2009).

Stomatal behaviour and stomatal based particular development are affected by drought in general. Water deficit can also influence the stomatal developmental programme in developing leaves. In Populus, drought affected stomatal traits as well as reducing conductance (Hamanishi et al., 2012). However, at the functional level, stomatal closure is an effective water saving mechanism but leads to decreases in intercellular CO2 and hence decreases in photosynthesis and possibly increases in leaf temperature. Stomatal responses to water status are not a passive response to dehydration but are driven by hydraulic and metabolic feedbacks (Buckley, 2019). Field drought, but there is also heat and high vapour deficit. In such a case of this natue, a low conductance phenotype could and certainly may be good for water saving but bad for particular evaporative cooling (Al-Salman et al., 2023). This highlights an important climate

change trade-off where the stomatal phenotype's improved drought tolerance may also increase heat vulnerability.

This trade-off is particularly significant for irrigated and rain-fed cropping systems. Conservative stomata may enhance water productivity under mild drought due to the compensation of the loss of carbon gain by a longer maintenance of leaf water potential. But at high heat stress, the same conservative phenotype can result in leaf temperatures beyond the optimum for photosynthetic enzymes, pollen development and membrane stability. This may lead to increased photorespiratory losses in C3 plants and diminish the thermal advantage that is usually associated with the pathway in C4 plants. Thus, evolution-based nature of stomatal density in response to basis of chronic water limitation may be an adaptation to frequency of drought here, while otherway stomatal kinetics and hydraulic capacity may determine survival during very short heat extremes (Al-Salman et al., 2023; Buckley, 2019).

Figure 1. Conceptual pathways linking climate change, stomatal traits, and photosynthetic efficiency in C3 and C4 plants

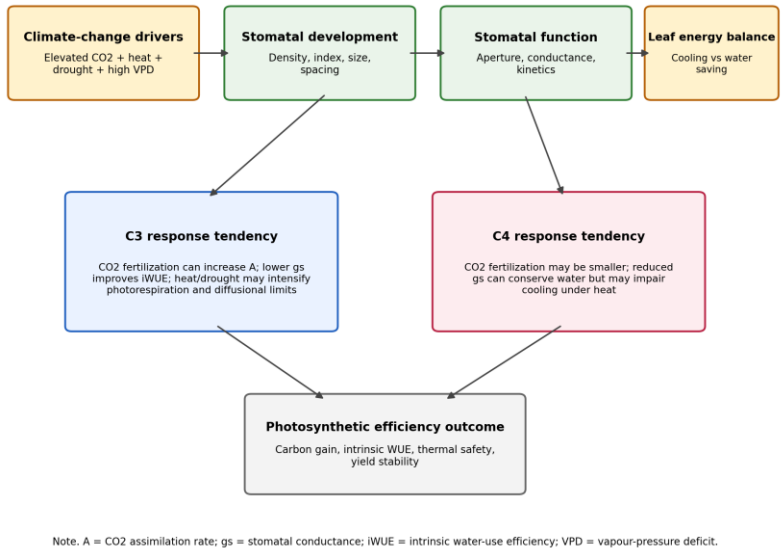


Figure 1: Conceptual pathways linking climate-change drivers to stomatal traits and photosynthetic efficiency in C3 and C4 plants

Comparative implications for C3 and C4 plants

In C3 species, climate change may initially enhance photosynthetic efficiency through CO2 fertilisation, particularly where nutrients and sink capacity are adequate. Reduced stomatal conductance would enhance intrinsic water-use efficiency and moderate density reductions would reduce water loss without excessive limitation to assimilation. However, under field conditions the realised CO 2 fertilisation effect is often lower than expected, due to nitrogen limitation, downregulation of Rubisco capacity, heat damage, ozone and drought (Ainsworth & Long, 2005; Leakey et al., 2009; Long et al., 2006). The most useful stomatal ideotype for C3 crops (including wheat, rice, soybean and potato) is likely to be one with a moderate density, rapid opening under sunflecks, rapid closure under shade or water deficit and co-ordination with mesophyll conductance and canopy cooling.

In C 4 plants, raised CO 2 does not typically stimulate photosynthesis via the same route, but stomatal closure may save water and postpone drought stress. Thus, C4 crops such as maize, sorghum, millet and sugarcane can be productive where water is limiting. However, if warming and heat waves are

predominant, the reduction in stomatal conductance may increase leaf temperature and decrease photosynthetic efficiency. Regulation of stomatal development also differs among C4 species. Comparative genomic and expression analyses here indicate that stomatal responses to drought are different between C3 and C4 crops and that based on current regulatory networks have evolved in a pathway-specific manner (Song et al., 2023). Thus, pathway identity is not sufficient for assuming C4 climate resilience. C4 plants generally perform well in high-light, warm environments, but their performance in future climates depends on the trade-off between saving water and keeping cool.

The difference can be summed up as a change in the main limiting factor. In C3 plants, diffusional and biochemical CO2 limitation is often strong so that stomata closure can be partly counterbalanced by elevated atmospheric CO2 under ambient CO2. In C4 plants, CO2 is biochemically concentrated close to Rubisco, thus a change in stomatal conductance affects transpiration more directly, and leaf temperature and hydraulic safety more directly, than the supply of the carboxylation substrate. This does not mean that stomata are unimportant in C4 species. Instead, their importance is shifted from providing CO2 to regulating the coupled carbon-water-energy economy of the leaf. Therefore, a breeding target should be tested under the combination of stresses expected in the production environment, be it high CO2 alone, CO2 plus drought, heat plus drought, or all three (Ghannoum, 2009; Liang et al., 2023; Xu et al., 2016).

Research and breeding priorities

The next research priority is linking stomatal anatomy with dynamic physiology. Although many climate experiments measure steady-state gas exchange, field photosynthesis occurs under conditions of fluctuating light, humidity, and temperature. Fast stomatal kinetics can increase carbon gain during transient light and reduce unnecessary water loss after irradiance declines (Lawson & Vialet-Chabrand, 2019; Sakoda et al., 2020). Therefore, high-throughput phenotyping should incorporate epidermal imaging, gas-exchange induction curves, thermal imaging, carbon isotope discrimination and drought-recovery assays.

Stomatal density by itself is a hazardous breeding aim. Reduced density can increase water-use efficiency, but too much reduction may reduce CO2 diffusion and leaf cooling. Higher density can improve photosynthetic induction under fluctuating light, but can also increase transpiration unless stomatal closure is fast. A more robust ideotype would combine: (a) pathway-specific combinations of density and size, (b) fast guard-cell kinetics, (c) mesophyll conductance matching stomatal supply, (d) root and hydraulic traits supporting leaf water status, and (e) canopy architecture buffering leaf temperature. Genetic tools that target stomatal development are promising but coordinated manipulation of stomatal and non-stomatal traits will be necessary for climate resilience (Franks et al., 2015; Lawson & Blatt, 2014).

Experimental design is as important. Many published studies use single stresses imposed for short durations. However, future field environments will involve sequential and simultaneous stresses. A good screening protocol would be to use leaves that develop in high CO2 and then experience fluctuating soil water and heat during functional maturity. Stomatal density and index should be reported separately, leaf surface specified, and stomatal size and pore area included, and anatomy related to assimilation, conductance, transpiration, and leaf temperature. Without this integration, density data can be statistically significant but biologically ambiguous.

Research/breeding gap	Why it matters	Suggested approach
Density measured without function	Stomatal density alone cannot predict conductance, photosynthesis, or WUE	Pair microscopy with gas exchange, thermal imaging, and stomatal-kinetic assays
Limited compound-stress studies	CO2, heat, drought, and VPD rarely act alone in the field	Use factorial experiments with realistic heat-drought timing and recovery phases
Pathway-specific ideotypes unclear	C3 and C4 plants differ in CO2 limitation, thermoregulation, and drought response	Compare C3 and C4 crops under shared protocols and include genotype-by-environment analysis
Steady-state bias	Field light and humidity fluctuate quickly; slow stomata reduce carbon gain and WUE	Phenotype induction and relaxation rates under fluctuating light and VPD
Weak integration with hydraulics	Stomatal closure depends on leaf water status and hydraulic transport	Combine stomatal traits with root depth, leaf hydraulic conductance, and canopy temperature

Table 2: Key research gaps and practical approaches for climate-resilient stomatal phenotyping and breeding

Conclusion

Climate change influences stomatal density and photosynthetic efficiency through interacting CO2, temperature, drought and vapour-pressure pathways. In C3 plants, photosynthesis and water-use efficiency are frequently enhanced by elevated CO2, but the advantage is limited by acclimation, nutrient limitation, drought and heat. C4 plants have lower direct CO2 fertilisation, but reduced stomatal conductance can save water and enhance productivity during drought; but the same reduction can be detrimental to evaporative cooling during heat stress. Stomatal density is thus a useful but incomplete climate-response trait. Its significance is related to stomatal size, aperture, kinetics, hydraulic status, mesophyll conductance and photosynthetic pathway. Future crop improvement for climate resilience should move from static density counts to integrated stomatal ideotypes optimising carbon gain, water saving and thermal safety under compound stress. A pathway-aware framework therefore can guide researchers to avoid over-interpretation of density alone and instead assess whether a stomatal phenotype guards productivity, water status, and leaf temperature in the same target environment.

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