Rice production threatened by coupled stresses of climate and soil arsenic

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Projections of global rice yields account for climate change. They do not, however, consider the coupled stresses of impending climate change and arsenic in paddy soils. Here, we show in a greenhouse study that future conditions cause a greater proportion of pore-water arsenite, the more toxic form of arsenic, in the rhizosphere of Californian Oryza sativa L. variety M206, grown on Californian paddy soil. As a result, grain yields decrease by 39% compared to yields at today’s arsenic soil concentrations. In addition, future climatic conditions cause a nearly twofold increase of grain inorganic arsenic concentrations. Our findings indicate that climate-induced changes in soil arsenic behaviour and plant response will lead to currently unforeseen losses in rice grain productivity and quality. Pursuing rice varieties and crop management practices that alleviate the coupled stresses of soil arsenic and change in climatic factors are needed to overcome the currently impending food crisis.
With more than half of the world’s population depending on rice for subsistence, it is crucial to ensure future rice production. Current empirically derived and modelled projections on rice production account for climate change as a constraining factor to yields. However, they do not consider the coupled stresses of climate change and the presence of arsenic, a plant and human toxin, in paddy soils.

The two determinants of climate change, elevated atmospheric CO$_2$ and temperature, have opposing effects on plant growth and performance. Increasing atmospheric CO$_2$ stimulates the photosynthetic rate of rice, increasing water and nutrient use efficiency and allocation of more photosynthetic product to the root, ultimately resulting in greater biomass and increased yields. Increasing temperature above the plant’s optimum, contrastingly, decreases photosynthetic rate, thereby reducing biomass yields.

Temperature often overpowers positive CO$_2$ effects, decreasing grain yields as a result of diminished grain filling. Besides affecting crop yields, climatic parameters also affect nutrient and contaminant behaviour in soils, thereby potentially altering the extent of their uptake into crops. The most relevant contaminant in flooded rice paddies is arsenic—it occurs ubiquitously, and naturally, in paddy soils globally, and is often found in groundwater used for irrigation. Furthermore, paddy soils irrigated with arsenic-contaminated groundwater accumulate arsenic with each successive irrigation cycle, exacerbating the effects of contamination with time.

In the soil, flooding induces reductive dissolution of iron oxyhydroxide minerals and reduction of arsenic adsorbed on soil minerals, increasing dissolved concentrations, and thus, plant availability of arsenic. Furthermore, sulphate-reducing and other methylation microbial communities in the soil methylate arsenic in a stepwise and reductive manner to mainly monomethylarsenic acid (MMAs(V)), dimethylarsinic acid (DMAs(V)), and trimethylarsine oxide (TMAs(V)O), which accumulate in rice grain. Methylated arsenic species are taken up more slowly into rice compared with inorganic species, but they are more readily translocated to the grain. Once taken up, arsenic diminishes plant growth and development, reducing grain yields and inhibiting both panicle development and grain filling. Even though methylated arsenic is carcinogenic, it is considered a less toxic variant of arsenic, and thus international regulation of arsenic contents in foodstuff only consider inorganic arsenic.

Increased temperature, and to a lesser extent increased atmospheric CO$_2$, will affect soil biogeochemical processes by altering the extent of their uptake into crops. The most relevant contaminant in flooded rice paddies is arsenic—it occurs ubiquitously, and naturally, in paddy soils globally, and is often found in groundwater used for irrigation. Furthermore, paddy soils irrigated with arsenic-contaminated groundwater accumulate arsenic with each successive irrigation cycle, exacerbating the effects of contamination with time.

While providing tight climatic control, our experimental approach imposes a restricted rooting depth and volume of water exchange (see discussion on utilising a greenhouse pot approach over other options in Supplementary Discussion 1). As a consequence, biogeochemical processes increasing (or decreasing) pore-water concentrations will be amplified with concomitant impacts on rice plants. Utilising soil arsenic concentrations within the lower range of documented levels for major rice-growing regions helps mitigate amplified arsenic concentrations resulting from reductive dissolution. Further, we used the same soil with two different arsenic contents to minimise biases towards differences in soil properties. Previous work demonstrated increased straw arsenic levels in pot studies, but similar grain arsenic contents compared with field trials. Our study design followed Dittrmar et al., who had compared pot and field studies with the same soil and found similar arsenic contents in straw and grain of rice. Moreover, we compare our rice yields for varying climatic conditions to field trials to ensure comparable outcomes. Nevertheless, our findings may not represent quantitative trends for field production; they will, however, provide critical information on the processes impacting future rice production globally and qualitative (direction of) changes to future yields and grain quality.

**Results**

**Determinants of grain yield.** Under today’s climatic conditions with a low soil arsenic content, the rice variety M206 produced 76% grain filling (Fig. 1) with grain filling of ~90% (Supplementary Fig. 2a). A shift to future climatic conditions (38 °C, 850 ppmv CO$_2$) alone resulted in a 16% yield loss (9.6 ± 1.2 g of grain plant$^{-1}$) with 76% grain filling, while increased total soil arsenic alone caused a yield loss of almost 40% (6.9 ± 0.9 g of grain plant$^{-1}$) with 96% grain filling. The combined impacts of changing climatic conditions and increased soil arsenic resulted in a 42% decrease in yield to 6.6 ± 0.5 g of grain plant$^{-1}$ with 81% grain filling. The interaction between soil arsenic and climatic conditions gave a p-value of 0.07 with ANOVA analysis, indicating a non-significant or weak interaction between soil arsenic and climatic conditions.
and climatic condition impacts on grain yield. The two climate factors, elevated temperature and elevated atmospheric CO₂, have opposing impacts on grain yield. Elevated temperature decreased grain yield by 13% (10.0 ± 0.7 g of grain plant⁻¹) with 83% grain filling, while elevated atmospheric CO₂ increased grain yield by 9% (12.4 ± 0.9 g of grain plant⁻¹) with 85% grain filling. In combination with arsenic, elevated temperature decreased grain yield by 65% (4.0 ± 0.7 g of grain plant⁻¹) with 58% grain filling, while elevated CO₂ resulted in a loss of 24% (8.7 ± 1.1 g of grain plant⁻¹) with 91% grain filling.

Under today’s climatic conditions with a low soil arsenic content, variety M206 had 5.9 ± 0.2 panicles per plant (Supplementary Fig. 2b). A shift to future climatic conditions alone did not affect the number of panicles per plant, while total soil arsenic alone decreased them. The combined impacts of changing climatic conditions and increased soil arsenic decreased the panicule number to the same value as soil arsenic. The two climate factors (elevated temperature and elevated atmospheric CO₂) had opposing impacts on the number of panicles per plant. Under low and high soil arsenic conditions, elevated temperature decreased, while elevated atmospheric CO₂ increased, the number of panicles per plant. Under today’s climatic conditions with a low soil arsenic content, 102 ± 6.3 spikelets were produced per panicle, which was adversely affected by an increase in soil arsenic (Supplementary Fig. 2c).

Unfilled spikelets of variety M206 contained 0.70 ± 0.07 µg As kg⁻¹ spikelet when grown under today’s climatic conditions with a low soil arsenic content (Supplementary Fig. 2d). A shift to future climatic conditions alone increased the arsenic content of unfilled spikelets, while total soil arsenic alone increased the arsenic content of unfilled spikelets even more. The combined impacts of changing climatic conditions and increased soil arsenic increased the amount of arsenic in unfilled spikelets most. The two climate factors elevated temperature and elevated atmospheric CO₂ impacted spikelet filling oppositely. Under low and high soil arsenic conditions, elevated temperature increased, while elevated atmospheric CO₂ did not affect the arsenic content of unfilled spikelets. Under today’s climatic conditions with a low soil arsenic content, the individual grain weight of M206 was 23.56 ± 0.36 mg (Supplementary Fig. 3). A shift to future climatic conditions alone did not affect individual grain weight, same as an increase in total soil arsenic alone. The combined impacts of changing climatic conditions and increased soil arsenic did also not affect individual grain weight. The two climate factors, elevated temperature and elevated atmospheric CO₂, impacted individual grain weight oppositely. Under low and high soil arsenic conditions, elevated temperature decreased, while elevated atmospheric CO₂ slightly increased individual grain weight.

The harvest index indicates how much energy is invested in vegetative compared with reproductive growth. Under today’s climatic conditions with a low soil arsenic content, the harvest index of variety M206 was 0.5 ± 0.0 grain to green biomass (Supplementary Fig. 4). A shift to future climatic conditions alone decreased the harvest index with an increase in straw biomass and decrease grain yield, while total soil arsenic alone did not affect the harvest index. The combined impacts of changing climatic conditions and increased soil arsenic decreased the harvest index to the same level as climatic change alone. The two climate factors elevated temperature and elevated atmospheric CO₂ again have opposite impacts on the harvest index. Under low and high soil arsenic conditions, elevated temperature decreased, while elevated atmospheric CO₂ hardly affected the harvest index of variety M206.

Determinants of grain quality. Under today’s climatic conditions with a low soil arsenic content, dehusked but bran-containing grains from rice variety M206 contained a total of 393 ± 16.9 µg As kg⁻¹ grain, of which ~250 µg As kg⁻¹ grain was inorganic arsenite (Fig. 2; Supplementary Table 2). A shift to future climatic conditions alone increased the total grain arsenic content to 580 ± 21.0 µg As kg⁻¹ grain with the contribution of inorganic arsenic doubling in the grain to ~450 µg As kg⁻¹. With increased total soil arsenic alone, the total amount of arsenic in the grain increased to 821 ± 30.4 µg As kg⁻¹ grain with the contribution of inorganic arsenic remaining at ~250 µg As kg⁻¹ grain. The combined impacts of changing climatic conditions and increased soil arsenic resulted in a total grain arsenic increase to 1004 ± 17.9 µg As kg⁻¹ grain with ~400 µg As kg⁻¹ being inorganic arsenic. The interaction between soil arsenic and climatic conditions gave a significant p-value of 0.008 with ANOVA analysis, indicating that soil arsenic and climatic condition also impact grain quality interactively. The two climate factors, elevated temperature and elevated atmospheric CO₂, impacted grain arsenic content differently. Elevated temperature alone increased inorganic and organic grain arsenic content similarly to future climatic conditions, while elevated atmospheric CO₂ alone resulted in a similar inorganic and organic grain arsenic content.
Fig. 2 Arsenic contents in *Oryza sativa* L. cv. M206 grains produced under different climatic and soil arsenic conditions. **a** Amount of organic (upper bar) and inorganic (lower bar) arsenic accumulated in dehusked grains produced under today’s (grey), future (purple), elevated CO$_2$ (blue) and elevated temperature (red) climatic conditions with low (solid) and high (chequered) soil arsenic levels. Upper green dashed line represents the European Union limit of 250 µg inorganic arsenic kg$^{-1}$ in husked rice, and the lower green dashed line represents the European Union and United States limit of 100 µg inorganic arsenic kg$^{-1}$ in infant food. **b** Arsenic species (arsenite and DMA) X-ray fluorescence micrographs of husked grains produced under today’s and future climatic conditions with high soil arsenic levels. Scale bar 500 µm. **c** Amount of arsenic accumulated in husk, and **d** percentage of arsenic retained by husk compared to amount of arsenic that entered the grain. (Eight biological replicates, mean values ± standard errors were compared to each other using the unpaired t test at a 95% confidence interval. Different lowercase letters indicate that mean values were significantly different from each other ($p < 0.05$), for details see Supplementary Table 2b, c, d)
as grains produced under today’s climatic conditions. In combination with arsenic, elevated temperature increased the inorganic grain arsenic fraction similarly as under future conditions, while elevated CO2 showed a similar inorganic arsenic content as under today’s climatic conditions.

Under today’s climatic conditions with a low soil arsenic content, the husk contained 166 ± 70.3 µg As kg⁻¹, which made up 31% of the arsenic moving into the grain (Fig. 2). Either a shift to future climatic conditions alone or an increase in total soil arsenic content increased the arsenic content of the husk (alongside increased arsenic retention by the husk). The combined impacts of changing climatic conditions and increased soil arsenic enhanced the arsenic content of the husk to the same level as an increase in soil arsenic alone. The two climate factors, elevated temperature and elevated atmospheric CO2, impacted the harvest index differently. Under low soil arsenic conditions, elevated temperature increased the arsenic content of the husk, while elevated atmospheric CO2 did not affect the amount of arsenic in the husk. Under high soil arsenic conditions, elevated temperature increased the arsenic content of the husk, while elevated atmospheric CO2 did not affect the amount of arsenic in the husk.

Rhizosphere arsenic and iron dynamics. Three and a half times-higher total arsenic concentrations in the soil resulted in four-times higher dissolved pore-water concentrations of 4.12 ± 0.89 mg L⁻¹ compared with 1.04 ± 0.12 mg L⁻¹ (Fig. 3; Supplementary Table 4). Climatic change alone increased the dissolved pore-water concentration to just 1.65 ± 0.09 mg L⁻¹, although higher pore-water concentrations (and thus plant root exposure) occurred before week 8 in the growth cycle of the plant. Increasing temperature, and to a slight extent increasing atmospheric CO2 concentrations, further exacerbated the partitioning of arsenic from solids to pore-water with respective 6.98 ± 0.59 and 5.13 ± 0.40 mg L⁻¹. Overall, temperature lead to highest dissolved arsenic exposure at earlier growth phases of the plant compared with elevated atmospheric CO2 concentrations. After 8 weeks of plant growth, dissolved arsenic concentrations were similar for all climatic conditions, varying only with the total arsenic content in the soil.

In addition to an increase in dissolved arsenic concentrations and a shift in arsenic exposure timing under future climatic conditions, the proportion of arsenite, a trivalent species of arsenic more toxic to humans compared with the pentavalent form arsenate, in pore-water also changed (Fig. 3). While 92.3 ± 8.7% of pore-water arsenic was arsenite under today’s low arsenic conditions, arsenite accounted for 97.0 ± 6.0% under future climatic conditions with low arsenic levels in the soil. At higher soil arsenic concentrations, 74.9 ± 4.4% of the arsenic was present as the arsenite species under today’s climatic conditions (as expected as the soil was spiked with 70% arsenite and 30% arsenate), compared with 89.4 ± 14.0% under future climatic conditions. Temperature as the sole climatic variable shifted the
proportion of arsenite to 96.4 ± 6.2% of total pore-water arsenic, while elevated atmospheric CO₂ alone decreased the proportion of arsenite to 65.1 ± 3.5%.

Iron concentrations in the pore-water generally increased before week 8 in the growth cycle of rice M206, while it reached the same level under all climatic and soil arsenic conditions during the reproductive phase of the plant (Supplementary Fig. 5). Under low soil arsenic conditions, elevated temperature alone and combined future climatic conditions increased pore-water iron concentrations, with the timing of highest pore-water iron concentrations pushed towards the beginning of plant growth cycle. Under elevated atmospheric CO₂ conditions, the amount of iron in the pore-water also increased compared with today's climate, although the timing of iron release remained the same. At high soil arsenic conditions, the response of pore-water iron dynamics was less pronounced.

**Microbial and carbon dynamics.** We used 16S rRNA gene copy numbers g⁻¹ dry soil to approximate changes in microbial community cell numbers (Supplementary Fig. 6a). In comparison with today's climatic conditions with a low soil arsenic content, future climatic conditions with a low soil arsenic content resulted in an intermediate decrease in cell numbers. High soil arsenic levels alone decreased cell numbers compared with low soil arsenic conditions. Future climatic conditions combined with high soil arsenic levels exhibited similar cell numbers as under future climatic conditions alone. While increased temperature alone resulted in a strong decrease in cell numbers, elevated atmospheric CO₂ alone caused a slight decrease.

Dissolved organic carbon within the rhizosphere pore-water was impacted most appreciably by temperature (Supplementary Fig. 6b). Plants grown at elevated temperature or under future climatic condition had nearly twice as much DOC compared with the rhizosphere for today's climate or under elevated CO₂ conditions. High soil arsenic suppressed the differences, where slightly greater DOC occurred for lower temperature conditions and slightly less DOC occurred at higher temperature relative to low soil arsenic conditions. Similarly, for low soil arsenic, dissolved inorganic carbon (DIC) was impacted most appreciably by temperature, being highest for elevated temperature conditions and then future climate conditions (Supplementary Fig. 6c). High soil arsenic altered the controlling influence of growth conditions; temperature effects alone were muted, but the combination of elevated CO₂ and increased temperature of future climate conditions resulted in the greatest DIC.

**Discussion**

Under today's climatic conditions with a low soil arsenic content, the observed yield of rice variety M206 grown under greenhouse conditions is in accordance with reported performance in California. A decrease in yield of ~16% under future climatic growth conditions (38 °C, 850 ppmv CO₂) alone has also been reported in empirically determined and modelled rice production studies, although these studies are not specific to rice variety M206. As previously reported, most of that loss is due to temperature stress, which can only partially be counteracted by elevated atmospheric CO₂. A loss of 39% grain yield due to increased total soil arsenic alone is also consistent with previous findings. Critically, soil arsenic accounts for nearly twice as much grain loss as combined temperature and CO₂ changes, indicating that under conditions tested here, arsenic is a stronger determinant of yield than climate. Thus, the combined impacts of changing climatic conditions and increased soil arsenic cause a loss of 42% decrease in yield, which is not compensated by elevated CO₂.

Variations in grain yield under different growing conditions are driven by differing impacts of arsenic and climatic stresses on plant physiological traits and rhizosphere dynamics. Overall, soil arsenic (at the concentrations examined) did not affect individual grain weight; it did, however, decrease the number of panicles per plant and spikelets per panicle. By contrast, temperature decreased individual grain weight as observed previously, and reduced spikelet filling, especially when combined with soil arsenic stress. Elevated temperature combined with higher soil arsenic levels increased arsenic concentrations in unfilled spikelets, indicating that these arsenic levels inhibited grain filling in spikelets. Under climatic stress, variety M206 invested more energy in vegetative compared with reproductive growth, indicated by a lower harvest index, which was unaffected by soil arsenic alone. Soil arsenic had a principal effect of decreasing overall plant productivity.

The observed effects on rice performance with increased soil arsenic concentrations is caused by an increase in dissolved pore-water concentrations in the rhizosphere that lead to increased plant arsenic accumulation and increasing temperature. Further exacerbates the partitioning of arsenic from solids to pore-water, stimulating the reductive dissolution of As-bearing Fe(III) (hydr) oxides as indicated by increases in pore-water arsenite and iron concentrations. Thus, rice plants are exposed to higher arsenite concentrations at earlier growth stages. Increasing atmospheric CO₂ concentrations also stimulated microbial respiration in the rhizosphere (increased inorganic pore-water carbon) causing reductive dissolution of Fe(III) (hydr)oxides and arsenite oxidation, as indicated by increases in iron and arsenate concentrations.

Our study imposed a rapid temperature and CO₂ transition that would otherwise transpire over the coming decades. As a result, the microbial community may not evolve comparably despite most organisms having a rapid doubling time and prior acclimation of the soil to high arsenic and climate for a season. In our study, bacterial numbers decreased significantly due to a rise in temperature, which was only partially recovered by elevated atmospheric CO₂ under future climatic conditions. Nevertheless, the functional indicators of microbial activity (inorganic carbon pore-water concentrations of redox active elements) for arsenic are entirely consistent with expectations; an increase in temperature and/or atmospheric CO₂ will lead to increases in organic carbon exudation from plants and microbes (shown by increased organic carbon in pore-water) and increases in microbial activity, as noted by the DIC levels, and thus, greater oxygen demand and greater As(V)/Fe(III) reduction with increases in temperature.

Climate and arsenic imprints on grain yield are, however, only half of the story; their coupled impacts on grain quality (inclusive of toxin and nutrient content) also are critical for consideration. Dehusked but bran-containing grains from rice grown under current climatic and soil arsenic conditions contained a total of 393 ± 16.9 µg As kg⁻¹ grain. Comparable inorganic arsenic levels (between 100 and 400 µg kg⁻¹ grain) have been reported for grains without husk and without bran of Californian grown white rice. In fact, and in accordance with the present study, unpollished white grain has been reported to contain more arsenic compared to polished grain. Nonetheless, differences in arsenic accumulation in the grain have been reported and debated when rice is grown in pots compared with fields due to maintaining a constant head of flood water in the pots rather than variable and dynamic flooding and draining conditions in the field. Our results may thus magnify the effect of future climate change, but the forcing of increased arsenic mobility, changes in speciation and coupled physiological plant stress with increased temperature will impact rice yields and grain quality consistent with our findings.
For rice variety M206, arsenic passed the bran and entered the endosperm of the grain more extensively under future climatic conditions. In fact, higher temperatures doubled inorganic arsenic in the grain, while organic arsenic concentrations remained unchanged. This is consistent with Arao et al.5,2, who showed that higher air temperature in the late ripening stage of rice increased inorganic arsenic in the grain. Overall, the change in climatic conditions did not affect the organic arsenic content in the grain, and similarly did not affect DMA in pore-water (Supplementary Fig. 7). Increased soil arsenic, however, leads to greater organic arsenic concentrations within the grain without notable change in inorganic arsenic, consistent with previous findings5,6,6. The higher soil arsenic concentration lead to a saturation of total arsenic within the grain, thus shifting the species of arsenic from organic to inorganic under elevated temperature and future climatic conditions. Governmental guidelines for arsenic levels within food, in fact, focus on restricting inorganic arsenic. Therefore, even without a change in soil arsenic concentration, climate change and most notably temperature, will cause grain inorganic arsenic levels to increase. In fact, under a future climate, more DMA is retained by the husk, preventing DMA from entering the bran. The combined impacts of high soil arsenic and high temperature, however, appear to saturate husk retention and lead to greater arsenic levels reaching the grain. Thus, overall grain toxicity to humans will increase under a shifting climate.

Collectively, our findings illustrate that for *Oryza sativa* L. variety M206, soil arsenic concentrations are major determinants of rice yield, with increasing soil arsenic levels having an overriding impact on yield decreases, while temperature combines to result in large increases in inorganic arsenic levels within rice grains. The doubling of inorganic arsenic in rice grain at any soil arsenic concentration with temperatures increases of 5 °C severely enhances the potential for human dietary exposure to arsenic, especially when considering that infant food levels for arsenic in the United States and the European Union are regulated to be <100 μg As kg⁻¹ grain. Extrapolating from the Californian rice variety M206 and Californian paddy soil to other varieties and soils, assuming that the direction of response to climate and soil arsenic stresses will be similar even if different in magnitude, leads to the important conclusion that rice grain yield and quality losses will result from interlinking soil arsenic and climatic drivers. Thus, factors considered for predictions of future rice productivity need to be expanded to paddy soil arsenic contents coupled with assessment of future climatic conditions. Grain quality assessments should consider not just soil arsenic but climate-associated influences on soil biogeochemical cycles that influence toxin levels in rice grains. Current endeavours of plant breeding seek either climate- or arsenic-resistant varieties, though seeking rice varieties that minimise arsenic yield impacts and managing paddy soils to limit temperature-induced changes to arsenic speciation and plantavailability will be needed to limit the effects of the coupled arsenic-climate impact on rice.

**Methods**

**Soil and characterisation.** Paddy soil and rice grains were obtained from a rice farm near Arbuckle, California (39°01'38.2"N 121°55'36.7"W, elevation: 22 m) in June 2016. Rice grains *Oryza sativa* L. sub-species japonica, cultivar Calrose, variety M206 were produced in 2015. Paddy soil texture was determined in triplicates at 20 °C by mixing ~75 g of air dry soil with 100 ml of 50 g L⁻¹ sodium hexametaphosphate (Na₂PO₄), analytical grade) and topped up to 1 L with water. The fraction of sand was quantified with a hydrometer after 40 s, silt after 2 h, and the remaining fraction was calculated as clay. Soil pH was quantified in triplicates from air-dried soil with double-distilled water at a 1:5 w/v ratio after 2, 24 and 48 h at room temperature. The elemental content of the soil was quantified with X-ray fluorescence (XRF, Spectro XEPOSitive HE XRF Spectrometer, AMETEK, Germany) from 5 g of freeze-dried soil. The cation exchange capacity was quantified in triplicates from air-dried soils with 0.1 M BaCl₂ (analytical grade) at a 1:25 w/v ratio for 4 h at room temperature. Inductively coupled plasma–optical emission spectroscopy (ICP-OES, iCAP6000, Thermo Scientific, UK) was used for quantification of the extracted elements. The total carbon and nitrogen content were determined in triplicates from air-dried soils by combustion in tin foil boats (Carlo-Erba NA 1500, USA). 0.5 M HCl (analytical grade) extractable elemental fraction was quantified with ICP-OES and ferrozine for Fe(II)/Fe(III) speciation after extraction of air-dried soil at a 1:40 w/v ratio for 1 h at room temperature. To amend the paddy soil with arsenic, wet field soil was mixed with autoclaved double-distilled water containing 80% arsenite (Na₂HAsO₄, analytical grade) and 20% arsenate (Na₂H₂AsO₄·7H₂O, analytical grade) (see Supplementary Table 1). Thus, soil arsenic concentrations varied from a background value of 7.3 mg As kg⁻¹ dry soil to 24.5 mg kg⁻¹. The soil was left to equilibrate for 4 months at the specific climatic and radiative conditions for rice. Arsenate and arsenite adsorb at the oxide surface of the rice, and subsequently reaching steady-state pore-water concentrations within hours; even with the maturing of arsenic–iron precipitates, steady-state dissolved concentrations are reached within 3 months5,6. Thus, our pre-incubation time allows ample time for arsenic to bind to mineral surfaces and reach conditions similar to field settings.

**Greenhouse design.** Rice was grown under controlled environmental conditions in growth chambers (polycarbonate, 1.2 × 1.8 × 1.8 m) within two larger greenhouses (Supplementary Fig. 1). Each greenhouse contained four growth chambers: one exhibiting today’s climatic conditions found in Californian rice-growing regions (33 °C average high daytime temperature during rice-growing season from May to September) and atmospheric CO₂ of 415 ppmv), one with future climatic conditions according to the RCP 8.5 scenario of the latest IPCC report11 (38 °C and atmospheric CO₂ of 850 ppmv) and two growth chambers with either climate parameter (elevated CO₂ or elevated temperature). Outside air was fed into the centre of each chamber through a fan running at ~10 L of air s⁻¹, exchanging the entire atmosphere of the growth chamber ten times per hour. Air exited the growth chamber through a top vent. To achieve doubled atmospheric CO₂ contents in future chambers, and elevated CO₂ in growth chambers, 99.9% Linde (Praxair Inc.) was injected continuously directly into the inflowing air at the mouth of the fan. CO₂ flow was monitored in one chamber every second with an infra-red gas analyser (Gasohound LI-820, LI-COR Inc.), and adjusted simultaneously for all four high CO₂ chambers using mass flow controllers (Tylan FC-260, International Process Control Inc.) controlled digitally to analogue converters (SDM PA4, Campbell Scientific Inc.). The atmospheric CO₂ content was monitored in all chambers at two locations in between the rice plants using an infra-red gas analyser (LI-6262 CO₂/H₂O Analysier, LI-COR Inc.), which was calibrated every week. CO₂ in chambers with low CO₂ averaged 418 ± 27 ppmv over the season and 802 ± 27 ppmv in chambers with high CO₂.

The temperature within each chamber was controlled by heater fans (King Electric PHM-1 1500-Watt Portable Milkhouse Heater) connected to timers (digital timer 9520S, Chicago Electric); the heaters were operated within the growth chambers from the hours of 05:30 to 19:30.

Each chamber contained two water-filled basins (80 × 60 × 28 cm), in which rice pots were placed. Each water basin was heated constantly by 125 W of fully submersible aquarium heaters (JAGER TruTemp Aquarimeter, Eheim) to 5 °C lower temperatures compared with the atmospheric daytime temperature (i.e., 27 °C and 33 °C for low and high temperature chambers, respectively). Thus, night-time atmospheric temperature increased to 20 °C, and high temperature chambers between the hours of 19:30 and 05:30. Temperature and atmospheric CO₂ parameters were monitored and controlled with the programme LoggerNet 3.3.1 (Campbell Scientific Inc.), which was executed by the datalogger control unit CR10 (Campbell Scientific Inc.). An even temperature and atmospheric CO₂ distribution within each chamber was assured in pre-experimental climate runs of the greenhouse.

Normal light was supplemented with regular lights in the greenhouse between the hours of 06:00 and 19:00 to support naturally occurring sunlight and to minimise shading within each chamber. The photosynthetic photon flux density was between 300 and 600 μmol m⁻² s⁻¹ (equivalent to a photosynthetic active radiation of 65–130 W m⁻²) throughout the day, depending on the prevailing weather during the season.

**Experimental design.** Each growth chamber hosted microcosms with natural and amended soil arsenic levels, which were placed into either of the two water-filled basins (see Supplementary Fig. 1). The water-filled basins served two purposes; one to provide a lower and more constant temperature to the soil compared with the atmospheric temperature, and the second to maintain temperature differences in low and high atmospheric temperatures overnight. Rice pots (high-density polyethylene, 14-cm diameter, 18-cm height) were filled with ~3.4 kg of water-logged paddy soil to 4 cm below the rim. Rhizom samplers (19.21.25, Rhizosphere Research Products) were placed horizontally midway in each pot. Soil was flooded with tap water, pH 7, and irrigated continuously with pumps through a drip irrigation system using water from the basins.

Rice variety M206 was germinated in sterilised tap water under the different climatic conditions. After 1 week of germination, seedlings of similar shoot and root lengths were placed into pots. The soil was fertilised with urea (CON₄H₂, analytical grade) using 185 kg nitrogen ha⁻¹ at the beginning of the season, after 4.5 weeks of growth and at panicle initiation, according to practices performed by Californian farmers. Three plants were planted per pot and eight pots per
environmental condition, two independently run greenhouses with four climate chambers each. To minimise light, temperature and atmospheric CO2 biases due to placement of plants with respect to the interior of the greenhouse, plants were placed around within a barn, and chambers were switched every 3–4 weeks.

**Pore-water analysis.** Pore-water geochemistry was examined regularly by drawing pore-water through rhizo samplers into acid-washed, butyl-stopped and evacuated glass vials. The pore-water was filtered through 0.2-μm syringe filters in an anoxic chamber (98% N2/2% H2 atmosphere) and diluted in 2% nitric acid (analytical grade) for total elemental (As, Fe) quantification with ICP-OES. Pore-water organic carbon was quantified using the total organic carbon method (TOC) on a Shimadzu TOC-L analyser with in-line acidification (phosphoric acid). Once a month, an aliquot of the filtered pore-water was used to determine the pore-water pH, which remained constant during growth (data not shown). Arsenic speciation in the pore-water was analysed using an arsenic speciation cartridge (anion exchanger, Metalsoft, USA) and double-checked by ion chromatography (Dionex ICS-3000, Dionex Corp., USA, PRPX-100 column using a 10–40 mM NH4H2PO4 pH 5.6 gradient) coupled to ICP-MS (XSeries2, Thermo Fisher Scientific Inc., USA) (IC–ICP-MS). Using IC–ICP-MS, we found that DMA was present in pore-water, but only contributed to <3% to total arsenic, which was negligible for arsenic speciation changes. Negligible amount of As(III) was measured after every 15th sample to check for instrument signal drift. Mean and standard errors were calculated of all data set. The data analysis was performed using the StepOneTM 2.3 software. Each of these independent DNA extractions were measured in triplicates.

**X-ray fluorescence imaging.** The distribution of arsenic and other elements across husked rice grains was visualised with X-ray fluorescence (XRF) mapping using beamline 2–3 at Stanford Synchrotron Radiation Lightsource (SSRL). The beamline receives X-rays from a 1.3 Tesla Bend Magnet, and it is equipped with a double-crystal Si (111) monochromator for energy selection, a vortex silicon drift detector for maximisation chambers. The sample is positioned in a 45° angle to the incoming beam and another 45° angle to the detector (90° angle between incoming beam and detector). The Kirkpatrick-Baez mirror system achieves a beam size of ~2 × 2 microns. The beam was calibrated to the arsenic K-edge of an arsenate standard, and maps were run at the energy for arsenite, dimethylarsinic acid (DMA) and total arsenic,, at a 0.013-mm step size and a 45 ms dwell time. Mapping energies for arsenite and DMA were chosen as they contribute >95% to the respective inorganic and organic arsenic fractions in the grain (previously verified with IC–ICP-MS in grain extracts). Rice grains were split in half on the longitudinal axis of the grain and fixed on glass slides. One single replicate grain was run per climatic and soil arsenic condition. Using the software SMAX20, arsenic fluorescent counts were quantified to an arsenic standard of known concentration (47 μg As cm−2) and expressed in μg As kg−1 grain for a sample thickness of 1 mm and a grain density of 0.8 kg of grain L−1. Average fluorescent counts for DMA and arsenite were obtained for husks, brans and endosperm. DMA and arsenite ratios from the husk to bran, bran to endosperm and within husk, bran and endosperm were calculated.

**Data analysis.** Mean and standard errors were calculated of all data set. The data were verified for normal distribution with the Kolmogorov–Smirnov Test. Standard Student’s t tests were combined with a two-factorial ANOVA analysis to display significant differences in means of data and illuminate significant interactions between climatic condition and soil arsenic (Supplementary Table S2). The distribution of arsenic and other elements across husked rice grains was visualised with X-ray fluorescence (XRF) mapping using beamline 2-3 at Stanford Synchrotron Radiation Lightsource (SSRL). The beamline receives X-rays from a 1.3 Tesla Bend Magnet, and it is equipped with a double-crystal Si (111) monochromator for energy selection, a vortex silicon drift detector for maximisation chambers. The sample is positioned in a 45° angle to the incoming beam and another 45° angle to the detector (90° angle between incoming beam and detector). The Kirkpatrick-Baez mirror system achieves a beam size of ~2 × 2 microns. The beam was calibrated to the arsenic K-edge of an arsenate standard, and maps were run at the energy for arsenite, dimethylarsinic acid (DMA) and total arsenic, at a 0.013-mm step size and a 45 ms dwell time. Mapping energies for arsenite and DMA were chosen as they contribute >95% to the respective inorganic and organic arsenic fractions in the grain (previously verified with IC–ICP-MS in grain extracts). Rice grains were split in half on the longitudinal axis of the grain and fixed on glass slides. One single replicate grain was run per climatic and soil arsenic condition. Using the software SMAX20, arsenic fluorescent counts were quantified to an arsenic standard of known concentration (47 μg As cm−2) and expressed in μg As kg−1 grain for a sample thickness of 1 mm and a grain density of 0.8 kg of grain L−1. Average fluorescent counts for DMA and arsenite were obtained for husks, brans and endosperm. DMA and arsenite ratios from the husk to bran, bran to endosperm and within husk, bran and endosperm were calculated.

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Author contributions
This work was conceptualised by E.M.M. and S.F. Greenhouse work and plant and soil geochemical measurements were planned by E.M.M. with input from S.F. and carried out by E.M.M. and T.W. Synchrotron work was carried out by E.M.M. Rice grain arsenic speciation measurements were carried out by B.P.F. and C.K. The paper and supporting information were written by E.M.M. with primary input from S.F. and additional input from all co-authors.

Competing interests
The authors declare no competing interests.

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