Adapting crop production to climate change and air pollution at different scales

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Editor’s summary

Elevated CO_2, global warming, ozone pollution, and drought are major climate-related environmental challenges affecting field crop production. This paper discusses strategies and perspectives for crop production under climate change and air pollution at plant, field, and ecosystems scales.

Abstract: Air pollution and climate change are tightly inter-connected and jointly affect field crop production and agroecosystems health. Although the individual and combined impacts of air pollution and climate change factors are increasingly understood, adaptation of crop production to concurrent air pollution and climate change remains challenging. Here, we review the recent advances on the adaptation of crop production to climate change and air pollution at plant, field, and ecosystems scales. Main approaches at plant level include integration of genetic variation, molecular breeding, and phenotyping. Field level techniques include optimizing cultivation practices, promoting mixed cropping and diversification, applying technologies such as antiozonants, nanotechnology and -robot-assisted farming. Plant and field level techniques would be further facilitated by enhancing soil resilience, incorporating precision agriculture, and modifying the hydrology and microclimate of agricultural landscapes at the ecosystem level. Strategies and perspectives for crop production under climate change and air pollution are discussed.

Challenges of crop production under air pollution and climate changes

Since the introduction of semi-dwarf and disease resistant crop varieties during the green revolution [1], the yield potential of new cultivars in large regions has stagnated due to counteracting effects of climate change [2]. Such effects will likely continue impacting our cropping systems [3] and anthropogenic greenhouse gas emissions continue to rise [4]. Therefore, it is essential that methods of crop production are constantly revised and adapted according to the latest policies and contemporary environmental challenges.

Tackling climate change and air pollution is considered as one of the most urgent global tasks and affects sustainable development goals [5]. Elevated CO_2, global warming, ozone pollution, and drought are major climate-related environmental challenges [6]. Water deficit stresses cause stomata closure, reducing the ozone uptake and its damaging effect on photosynthesis in some cases [7,8]. Elevated CO_2 lowers the concentrations of several nutrients and vitamins, and threatens human dietary needs, such as B vitamins that are reduced by 17-30% in rice [9,10]. However, elevated CO_2 increases photosynthesis and crop growth, and can offset the negative impacts of heat stress [11]. Increasing CO_2 might also alleviate ozone impact due to smaller ozone uptake [12]. The positive effect of CO_2 on crop yields might be reduced depending on local microclimate conditions. Higher CO_2 concentrations in the surrounding air lead to enhanced intracellular CO_2 saturation, decreasing transpiration, and increasing internal water use efficiency [13]. At the regional and global scale, crop production is affected by these climate factors and their interactions with anthropogenic activities. For instance, the complex distribution of different cropping systems and landscape components, as well as their interactions between land and atmosphere strongly affect the climatic condition, i.e. drought [14], warming [15], and ozone concentration [16]. Moreover, the interactions between multiple stressors are highly complex and can lead to dynamic and non-linear impacts, including antagonism, additivity, and synergism [8]. Thus, adaptation strategies under climate change must incorporate positive or negative antagonistic, additive, or synergistic effects of the multiple environmental factors on crop physiological characteristics and crop production. Interactive effects of these stressors on crops might differ across spatial scales. Thus, understanding these interactions (additive, multiplicative, or compensating at different levels) is needed to provide suitable adaptive strategies. However, recommending adaptation options in responses to stressors remains challenging because those abiotic stress factors naturally occur together.

Here, we discuss potential solutions to adapt the crop production to climate change and air pollution at plant, field, and ecosystems scales (Fig. 1). We focus on adaptation to ozone, CO_2, and warming; however, other contemporary stressors are also considered in the discussion where adaptation strategies may offer additional benefits against such stressors.

Adaptation options at plant scale

Breeding approaches

Intraspecific genetic variation in resistance to climate change exists in different crops, which provides the basis for crop breeding [17,18]. Molecular breeding approaches such as marker-assisted selection (MAS) constitute a major leap compared to traditional and time-consuming breeding approaches such as pedigree selection [17,19]. Germplasm collections, such as the fully sequenced plant material available from the 3000 Rice Genomes Project [20] form a powerful resource, as they can be used for phenotypic sceening of populations representing the entire genetic diversity of crop species in specific stress environments. Subsequently, the genetic architecture underlying favorable adaptive traits can be readily dissected with the aid of the available genomic sequence information using approaches such as genome-wide association study (GWAS). As a prerequisite, free access to the gene banks curating germplasm collections, as well as sustainable funding and benefit sharing schemes for gene banks need to be ascertained by agreements such as the International Treaty on Plant Genetic Resources for Food and Agriculture (https://www.fao.org/plant-treaty/en/). Researchers can then acquire the material to identify adaptive loci for specific environmental stress conditions that will then be introgressed into elite varieties using MAS. Regarding heat stress, ozone stress, and elevated CO_2, quantitative trait loci (QTL) and candidate genes were identified in major crops, which form a prerequisite for MAS breeding [17,18,21]. However, large-scale marker-assisted breeding programs for resistance to ozone and effective utilization of elevated CO_2 are missing. Conversely, heat-tolerance rice breeding is ongoing at the International Rice Research Institute (IRRI) [22], which is expected to add new discoveries in the near future.

Dissecting and integrating genetic variations for adaptation

Recent research programs now offer new insights for ozone. QTL related to ozone resistance were identified in rice [23], maize [24], and wheat [25]. Transcriptomic responses of crops such as common bean, garden pea and soybean to ozone were explored [26,27]. These studies demonstrate that ozone tolerance in crops is a quantitative trait. A classical pedigree selection approach in different field locations might not lead to ozone tolerance due to the unpredictability and heterogeneity of ozone occurrence, and therefore marker-assisted breeding might be the most promising approach to introgress known ozone tolerant loci into established crop varieties.

Carbon source-sink relationships play a significant role in determining the plant ability to utilize elevated CO_2 that increases photosynthesis [28]. QTLs for source- and sink-related traits, including flag leaf traits, yield traits, and photosynthetic pigments under ambient and elevated CO_2 were identified in rice [29–31]. In legumes, physiological traits related to elevated CO_2 were dissected [32]. These known loci can be utilized in breeding programs toward efficient CO_2 utilization. In addition, classical breeding approaches such as pedigree selection take place under gradually rising CO_2 concentration and might thereby unintentionally lead to adaptation and high yields under elevated CO_2 levels.

Improved crop yields due to CO_2 ‘fertilization’ may be limited by CO_2-induced reductions in the maximum carboxylation rate and the maximum rates of electron transport [33]. Therefore, improving biochemical limitations to photosynthesis offers an opportunity to enhance crop productivity. Rubisco activity is also linked to chloroplast CO_2 concentration [34]. Improving mesophyll conductance can enhance CO_2 diffusion from sub-stomatal cavities to chloroplasts, as a target of increasing chloroplast CO_2 concentration and Rubisco activity [35]. Improving the speed of stomatal opening would be beneficial to enhance crop yields under elevated CO_2. Concurrently, variation in ozone sensitivity among plants is related to stomatal conductance [36], and reduction in stomatal conductance and ozone stomatal flux may serve as targets for climate change adaptation. However, stomata optimize CO_2 uptake while minimizing water loss [37]. Hence, breeding for ozone-tolerant cultivars with lower stomatal conductance may result in suppressed photosynthesis and yield. The trade-off between photosynthesis and stomatal conductance to improve leaf water use efficiency is linked to plant ozone tolerance. Accelerating the response of stomata to light is an efficient approach to improve water use efficiency, which is used to breed drought tolerant cultivars [38,39]. Optimized stomatal behavior to control the trade-off between photosynthesis and ozone flux is also an avoidance of elevated ozone [40]. Ozone tolerance is often related to the concentration of ascorbic acid in the apoplast and leaf tissue in crops such as wheat, soybean, and maize [27,41,42]. Therefore, regulating antioxidant levels could improve ozone tolerance [43]. Increases in leaf cell wall thickness, apoplastic pH, and leaf tissue ascorbic acid concentration also result in greater ozone detoxification by apoplastic ascorbate [44], which may provide an efficient approach to breed ozone-tolerant cultivars. However, manipulation of the leaf apoplast toward a more reduced redox state could have the unintended consequence of altering the plant ability to sense and respond to pathogen infection [45,46]. Hence, a more holistic approach is needed based on biological interactions. Moreover, adaptation options should allocate equal focus between yields and nutritional quality, especially considering the current threat of malnutrition in undeveloped and developing countries.

Crop heat stress tolerance is also complex, and threshold temperatures are species-specific [47]. Multiple loci for heat tolerance were identified in rice at the seedling stage [48,49] and reproductive stage [50–54]. In addition, 35 heat stress-responsive meta-QTLs and 45 candidate genes were identified in rice, facilitating marker-assisted heat-tolerant rice breeding [55]. Heat-responsive loci were also identified in wheat [56–58], maize [59–61], soybean [62], and lentil [63]. These advances facilitate the formulation of targets in developing long-term plans for mitigating current and future global warming impacts [64], especially for tackling the challenge of superior plants under multiple combined stresses.

Breeding crops for a future climate needs to address favorable and unfavorable interactions of CO_2 with increasing ozone and temperature [32]. However, it is challening to maintain a breeding environment in which all of these environmental factors are stably maintained for a classical selection approach. A solution to this problem could be physiological breeding [65], in which physiological traits that confer advantages in these environmental conditions are introgressed into target varieties. The International Maize and Wheat Improvement Center (CIMMYT) reported the consideration of physiological traits, such as canopy temperature or the normalized difference vegetation index (NDVI), in breeding programs leads to wheat varieties with enhanced performance in heat and drought environments [65]. Such data are also commonly collected at field scale (see also section ‘phenotyping-robot-assisted farming’), further indicating the nexus between plant and field levels. In addition, as stress tolerance is a quantitative trait, many loci should be combined in a process called QTL pyramiding in order to adapt crop varieties to multiple stress conditions [66]. Although this is still an elaborate process, the availability of genome sequences for all major crops has greatly facilitated the fast identification of genetic markers for such MAS schemes [66,67]. One possible challenge that needs to be overcome in QTL pyramiding is ‘linkage drag’ of agronomically unfavorable traits that could be closely associated with favorable adaptive traits. Another challenge could be confounding or even conflicting physiological effects of QTL, for example in the case of stomatal regulation. Precise crop engineering based on mechanistic understanding of adaptive traits may help to overcome these challenges [68].

Adaptation options at field scale

Cultivation techniques for air pollutants and climate changes

There has been limited advance regarding how cultivation techniques may mediate air pollution impacts. Because elevated ozone accelerates leaf senescence and suppresses the photosynthetic rate of flag leaves during later developmental stages [69], early sowing of winter wheat helps to effectively reduce the ozone stomatal flux. On the other hand, the occurrence of ozone peak levels depends on the weather conditions, and sowing timing should be adjusted according to local conditions. Crop management practices such as changing irrigation facilitate improved crop tolerance to ozone. However, such a practice should also account for CO_2 emissions, e.g. decreased water supply may decrease CO_2 emission [70]. Adjustment of water supply would reduce water use and increase water use efficiency, thereby reducing ozone uptake flux. Preliminary findings suggest straw addition may offer benefits to crops under ozone stress [71]. Straw and other organic amendments to soil can also decrease soil CO_2 emissions, potentially offering double benefits [72,73]. Potential benefits in crop production of using crop management practices should be assessed using modeling frameworks and field experiments with multiple factors [74].

Ozone alters soil microbial communities and root activity [75,76], thereby impacting crop N uptake and grain protein accumulation [77]. There are no consistent results on the combined effects of ozone and N on crops [78,79]. N fertilizer aggravates, slows down or does not alter the effects of ozone on crops [78,80]. Ozone can also increase the optimum N application rates, decrease crop N use efficiency, and increase the risk of N-related environmental problems, such as soil N leaching, aquatic eutrophication, and greenhouse gas N_2O emissions [80]. Therefore, the time, frequency, dose and type of fertilization need to be further optimized to improve the N uptake capacity and antioxidant capacity of crops to cope with ozone stress. Fertilization regimes should also consider the influence of CO_2 effects. For example, the negative effects of low soil N on grain quality may be exacerbated by elevated CO_2 [81]. Concurrently, some agronomic measures are applied to increase the N utilization efficiency and reduce environmental pollution, such as combined application of organic and inorganic fertilizers [82]. Further research is needed to investigate whether these agronomic measures are effective in mitigating ozone damage to crops, especially with concurrent elevated CO_2 and warming [83].

Optimization of agricultural land management may act against global warming. For example, under the Representative Concentration Pathway 2.6, current agricultural mitigation practices to increase soil organic carbon sequestration may decrease global temperature by up to 0.26 ºC, potentially favoring also soil water holding capacity and fertility [84]. Moreover, irrigation can offset crop production loss due to global warming projected by the 2050s, although >5% expansion of irrigation areas in warm regions is needed to fully counteract losses [85]. These suggest that multi-factorial studies are needed to optimize the cultivation techniques for concurrent adaptation to ozone, CO_2, and warming at field scale.

Diversification of cropping systems for adaptation

Nowadays farming systems often utilize crop rotation (growing different crops on the same field in successive growing season), intercropping (simultaneously cultivating two or more crops on the same field), and overall crop diversification (incorporating additional new crops or cropping systems to existing farmland) [86]. These systems aid in increasing crop diversity, reducing chemical pollution, repressing pests and diseases, enhancing soil health and nutrient and use efficiency, promoting benefits of soil microorganisms, and increasing yields [86]. Agroforestry also promotes diversification, mitigates climate change impacts, and facilitates ecosystem services and economic development [87–89]. Such diversifying practices have a great potential to enhance agricultural sustainability and promote resource savings. For instance, modifications in crop rotations and distributions (switching) can contribute 23-40% toward the targets of agricultural sustainable development in China by 2030 and facilitate global resource savings [90]. Among other benefitis, fertilizers (-532 to -10.9%), pesticides (-4.3 to -10.8%) and greenghouse gases (-1.7 to -7.7%) can be decreased while farmers incomes are increased (+2.9 to +7.5%) [90]. Similar to crops, a recent analysis of Canada's National Forest Inventory (NFI) data revealed that enhancing functional diversity of trees increases decadal soil carbon (32%) and nitrogen (50%) in the mineral horizon [91]. Hence, such structural changes in the agroecosystems, including agroforestry, are widely addressed in the agroecological literature and have the potential to serve as a key to adaptation [92–95]. However, the role of diversifying crop systems under air pollution with or without combined climate changes has received little interest and remains elusive.

Diversifying crop cultures from monocultures to multi-species cultures increases annual primary productivity, plant biomass, and seed yield, but can decrease harvest index, a side effect that may be attributed to the breeding of current cultivars for best performance in monocultures [96]. However, from a climate change adaptation perspective, having a lower harvest index is not necessarily negative, if yields are also higher, given that the additional biomass production is incorporated into the soil to increase carbon sequestration, obtaining adaptation benefits from higher soil organic matter (SOM). Hence, greater seed yield gains may be compromised by diversification of cropping systems with crop cultivars bred for monocultures [96], suggesting that breeding programs should be optimized for mixed cropping systems to improve crop yields under future climate change and air pollution. Richness loss of services-providing organisms such as pest predator and pollinator contributes up to 50% of the impacts of landscape simplification on ecosystem services, negatively affecting crop yields [97]. Hence, to sustain crop productivity and agroecosystem health, the diversity of services-providing organisms should also be sustained [98]. The enhancement of crop productivity by increased crop diversity are partly driven by changes in the composition of soil microbial communities, especially increased abundance of plant-growth promoting microorganisms such as Actinobacteria [99]. However, the effects of crop diversity on communities of soil microorganisms depend on soil conditions, such as fertilization and moisture [99]. However, the continuum soil microbes-crop diversity-crop productivity is not well understood [99], calling for more research to optimize the outcomes. Diversification of cropping systems can also decrease the inputs of agrochemicals in the agroecosystems, thus offering a sustainable intervention for environmental health [100]. Hence, conservation of on-farm crop diversification is a promising approach to enhance crop production across the world, including developing countries [98,101,102] in future climate change and air pollution scenarios.

A system with crop diversification can enhance water infiltration, water storage, and reduce water runoff [103], increasing cooling capacity of the canopy against heat events [104,105]. An intercropping system of potato with legumes facilitates reducing soil temperature and increasing crop water productivity and radiation use efficiency as compared to solo potato [106]. Cooling effects may minimize the negative effects of heat stress while stomata are still open, but this might harm crops due to an increased ozone uptake [7,107]. There is an increasing understanding of solo and interactive effects of elevated CO_2, ozone, and high temperature based on both modeling work [108–114] and experimental studies [115]. However, the tradeoff effects induced by mixture of canopy structure and crop diversification (i.e. in mixed cropping system) on various climate factors, particularly with ozone, and their interactions need future studies.

Emerging technologies and management

Ethylenediurea (EDU) is a synthetic chemical and antiozonant protecting numerous crops [46,116–119]. Potential application of antiozonants within agroecosystems in the future would require the selection of the application method [120], but more toxicological and ecotoxicological studies covering the entire spectrum of low and high dose effects (hormesis) are needed before it can be applied into the agroecosystems. Moreover, cost-benefit analyses are needed to optimize the application interval and concentration and amount relative to the desired yield benefits. A more efficient use of antiozonants would require the concurrent protection against air pollutants and climate changes. For example, pretreatment of rice (*Oryza sativa* L.) plants with calcium acetate led to higher rice yield under combined O_3 and heat stresses [121]. Similarly, preliminary results show that EDU can improve plant functionality under water deficit stress in O_3-polluted ambient air (*Fraxinus* ornus; [122]), adverse ambient O_3 stress combined with particulate matter deposition (*Triticum aestivum*; [123]), and O_3 phytotoxicity under elevated CO_2 (*Oryza sativa*; [124]), hinting to the possibility of antiozonant application under multiple environmental stresses. Recent studies provide evidence for nanomaterials-induced protection against O_3 [125,126], with mechanisms resembling those protecting against other oxidative stresses [118], suggesting that nanomaterials can provide protection against various air pollutants and climate changes that induce oxidative stress in plants. Therefore, future chemical engineering developments have the potential to facilitate the incorporation of greener technologies with a lower potential accumulation of residues in the environment [118].

Biostimulants represent an extremely broad category of biological products that enhance plant productivity by affecting plants directly and indirectly [127,128]. Biostimulants often enhance the quality of harvestable products and their nutritional value [129]. With the tremendous increase in the use of biostimulants in the agricultural sector in the recent years [130], their simultaneous protection against air pollution and climate change is promising. Considerable literature indicates their efficiency in mitigating abiotic stresses and their potential as a low-input tool of cropping management for more sustainable farming [131,132]. These deductions are substantiated by recent studies showing different biostimulants protecting crops against O_3 damage [133–135], which adds to the widespread evidence for protection against climate changes.

Melatonin is also a highly pleiotropic molecule produced by animals and plants, which affects numerous diverse functions and processes in plants, including the circadian rhythms and its crucial role in day/night cycles, growth, photosynthesis, and rhizogenesis [136,137]. Melatonin improves plants and edible plant products by ca.7-30% against various elements of climate change and pollution [136,137]. The efficient protection of melatonin against different types of stresses suggests its suitability as a plant protectant that can facilitate its incorporation into the agricultural practice. While melatonin is proposed as a biostimulant for crops and post-harvest products, multidisciplinary studies are needed to explore the links of the impact of its use among agricultural, food technology, human nutrition, and environmental health [138].

Priming accelerates and boosts the defense response during subsequent exposures and leads to induced resistance and/or tolerance to both biotic and abiotic stress, including major climate changes such as heat and drought [139–141]. Seed priming can decrease the cost required for treatments on the field and to considerably larger plants, thus being a resource- and labor-efficient approach that poses also minimal environmental risk [140,142]. Priming gives an additional benefit as it can be used to regulate the (a)synchronous occurrence of ontogenic stages that are particularly sensitive to air pollutants to seasonal peaks [143–145]. On-field application of seed priming leads to increased economic returns and decreased cost-benefit ratio, with the greatest outcomes obtained when priming is incorporated with other agronomic practices, such as fertilizer micro-dosing and row spacing [144,145]. The use of nanotechnology, i.e. application of nano-primers, can facilitate an even more eco-friendly and sustainable priming [143], to protect against a broad spectrum of environmental stresses associated with air pollution and climate change.

Phenotyping robots can conduct measurements of plant traits at a high throughput and precision rate and thus have a great potential to support data acquisition for a better understanding of plant reactions in a changing environment. Assessment by phenotyping robots can accelerate the breeding process and allows for a closer study of the effects of environmental factors on complex plant traits [146]. The combination of phenotyping robots with precision farming has a significant potential for more target-oriented inputs and reduced impact on ecosystems, such as by decreasing greenhouse gas emissions by site-specific application of fertilizers or plant protection measures [147]. Moreover, phenotyping can speed up the breeding process and reveal new genotypic differences [148,149]. Therefore, phenotyping robot-assisted farming can aid efforts to adapt to ozone, CO_2, and warming by offering fast and real-time large data, providing a framework for the integration of a more holistic view to mitigate climate change and develop climate-resilient cultivars.

Adaptation options at ecosystem scale

Enhancing soil resilience

Climate change factors, such as elevated CO_2, ozone and warming, negatively influence SOM content and soil biota activity, which may consequently affect soil fertility, crop productivity, and the environment. For example, although elevated CO_2 increases the net primary productivity [150], a lower SOM storage is expected because of the faster decomposition of SOM under elevated CO_2 [151]. Warming enhances native SOM loss via altering soil functional microbial communities [152]. For instance, warming and elevated ozone alone and in combination generate tradeoffs between arbuscular mycorrhizae and the host roots and stimulate organic carbon decomposition in nontilled soybean agroecosystems [153]. As a key indicator of soil resilience, SOM content determines the level of soil fertility to a great extent and thus crop yield [154,155].Therefore, the loss of SOM resulting from climate change will likely decrease soil resilience and productivity. Increasing soil carbon storage is a promising way of enhancing soil resilience to mitigate the negative effect of climate change on agriculture. Lots of practices have been used to maintain SOM storage in agriculture, such as applying organic fertilizers, conservation tillage, straw mulching, and intercropping [156]. Some of these measures, e.g. incorporating organic ammendments into agricultural soils, have been proved to be efficient in increasing soil fertility and crop productivity via soil carbon sequestration [157].

To achieve adaptation to climate change and air pollution, soil organic matter should be increased via a set of management practices such as cover crops, agroforestry, organic inputs, reduced tillage, varieties, mixed farming [158]. These would directly affect the functioning of agroecosystem, including autonomy, biodiversity, infiltration, soil protection, water retention, nutrient availability, and carbon sequestration [158]. Thereby, impacts from climate change and resource depletion decrease [158]. Altogether, these would lead to increased yield and net primary productivity [158].

Incorporation of remote sensing technologies

Recent developments in remote sensing satellites include the Fluorescence Explorer (FLEX), which will be able to measure chlorophyll *a* fluorescence emitted from plants at high spatial- and temporal resolution from space after its launch in 2024 [159,160]. Passive or sun-induced plant chlorophyll fluorescence (SIF) measurements are sensitive indicators of photosynthesis. Since photosynthesis is the process where CO_2 is transformed into substance, the fluorescence signal serves as an integrative indicator of ecosystem dynamics and the status of vegetation functioning. The launch opens new perspectives and adaptation options since the integrated Fluorescence Imaging Spectrometer (FLORIS) allows for valuable assessments of direct and indirect ecosystem functions integrating effects of elevated CO_2, increased air pollution, and global warming. In order to support the FLEX data and correct, e.g., aerosol influences, Sentinel-3 satellites have been chosen to serve as tandem partners [160]. The auxiliary data provided by Sentinel-3 will be included to improve models of future atmospheric CO_2 concentrations. FLEX high sensitivity will enable generating instantaneous data which has not been aggregated over a longer time period and several overflights. By obtaining precise databases of dynamic crop adaptation, remote sensing can guide precision agriculture for advanced planning, crop yield and health estimation, and agroecosystems management [161]. Nevertheless, high degree of dependence on technology may be compromised in conditions of low availability of energy that can be expected to increase in a context of resource depletion and increasing conflicts. For example, the ongoing Russo-Ukrainian War affects the food system more through its effects on energy prices than through the decreased crop production in the area [162].

Modified hydrology and microclimate of agricultural landscapes

Under drought stress, plants close stomata to reduce water loss, which is limiting the uptake of ozone by vegetation which consequently increases surface ozone concentrations [163,164]. Ecosystem-atmosphere interactions reduced ozone removal by water-stressed vegetation, which exacerbated ozone air pollution over Europe during 1960-2018 (Lin et al., 2020). Simulation studies showed that irrigation decreases surface ozone by 0–5 ppb in irrigated areas but increases them by 2–7 ppb over the surrounding non-irrigation areas. Irrigation largely affects ozone exposure, but local impacts depend on the seasonality of emissions and climate [111]. Large-scale irrigation has the potential to bring positive effects through flexibility to avoid ozone peaks by shifting cropping calendars under irrigation. However, under irrigation, crops are sensitive to ozone damage because stomata fully open, thus increasing ozone uptake [7]. For heat stress, the effect of irrigation is positive because its cooling effect helps to reduce canopy temperature and thus restrict the negative effects of heat stress [165,166]. However, a decrease in canopy temperature may prolong phenological processes in crops, thus affecting crop yields [167]. Moreover, increased water input through irrigation may result in significant sensitivity of the ecosystem CO_2 respiration during the vegetation period as well as relatively high releases of CH_4 and N_2O [14,168,169], which are major ozone precursors. These impacts might offset the positive effects of irrigation on regulating ozone [170]. However, how irrigation or related management measures affect biological or atmospheric processes, in particular ozone concentration, remains poorly investigated [171]. Freshwater use is considered a planetary process whose boundary can soon be trespassed, which presents the main problem related to irrigation expansion [172]. Moreover, changes in landscape patternsstrongly alternate the hydrological processes and, thus, water availability for irrigating cropland [173,174] might indirectly influence the ozone concentration at larger scales.

Modifying the microclimate has also a high potential for improving crop performance in changing environmental conditions. One measure of modifying the microclimate for field crops is the integration of woody species in cropping systems (such as agroforestry), or agricultural landscapes [175]. Trees typically have deeper root systems than annual crops and can increase air humidity and decrease air temperature [176]. Moreover, via hydraulic lift they can provide moisture in more shallow soil layers to annual crops [177]. The combination of lower temperatures and higher air humidity potentially facilitates the adaption to heat stress, enhances ozone degradation, and improves CO_2 assimilation. However, exploiting such synergies would require carefully balanced and locally adapted agroforestry systems that are technically feasible and economically profitable.

Crop growth modeling

Given the large spatial variation in changes of climatic factors and ozone pollution across different global crop production regions [178,179], adapting crop production at regional scale should be region-specific. Therefore, it is essential to assess the spatial-variation before developing adaptation strategies [180,181]. Crop growth models, which can simulate dynamics of crop-soil system as influenced by climate conditions, soil characteristics and crop management, have been widely used for assessing climate change impacts on crop productivity [182,183]. Some recent estimations of elevated ozone impact on crop production were mostly based on statistical regressions, which usually ignore the cultivar or regions differences in the responses of crop production [184]. Applying the crop growth models at regional scale provides the opportunity to estimate the integrated impacts of climate change and elevated ozone together [113]. Another potential application of crop models is evaluating the possible impacts of different adaptation strategies, focusing on crop management and cultivar shifting.

Crop growth models have been improved substantially to enhance the suitability across different climate change scenarios and different regions, especially through the efforts within the Agricultural Model Intercomparison and Improvement Project (AgMIP) [185]. However, most of the current improvements in crop growth models focused on simulating the impacts of climate variables (e.g. rising temperatures, extreme climate events, CO_2) [186]. Elevated ozone potentially interacts with climate factors (rising temperature, CO_2) on several important growth processes, especially on leaf photosynthesis leaf senescence and grain C/N dynamics [187,188]. Current crop growth models rarely incorporated these interactions, except some empirical factors that were recently introduced into the models to modify the leaf photosynthesis on senescence [189,190]. Modeling the effects of rising ozone and temperature on leaf stomatal, and subsequently on evapotranspiration and canopy temperature should be the priority, as they have important implications for quantifying the accumulation of leaf photosynthesis and water use to elevated CO_2 under future climate. Coupling modeling with field empirical data from different cultivars and their responses is also needed. Furthermore, modeling should also account for dynamic responses and non-linear phenomena to produce more reliable impact estimates [191,192].

Perspectives for crop production under climate change and air pollution

The herein analysis suggests that climate change may not necessarily result in lower yields across all crops and locations. This is partly due to ongoing countermeasures adopted by local governments as well as because of individual actions by farmers in an effort to increase crop yields and thus their income, although further efforts are clearly needed to maximize adaptation and resilience under concurrent climate changes and air pollution [64,90,94,193]. Future local adaptation would require its own specific extent of weather and air pollution predictors, but finer spatiotemporal resolution of integrated weather, air pollution and yield data should be achieved, especially to capture risks during the most critical crop growth stages [193].

The present analysis suggests that no single method or approach would suffice to adapt crop ecosystems to climate change and air pollution. A plethora of methods or approaches should be integrated considering not only crop productivity but also environmental impact, thus requiring cost-benefit analyses in terms of both agricultural and environmental sectors. The adaptation includes different scales, i.e. plant, field, and ecosystem (Fig. 1). However, a new generation of research programs is needed to move to more multidimensional researches in which different sets of methods and approaches at different levels (plant, field, ecosystem) would be tested as to benefits under combined environmental stressors (Fig. 2). Incorporation of key traditional strategies of agroecology, such as biodiversification, soil management and water harvesting, into agroecosystem management would facilitate increasing resilience while providing economic benefits [194].

Adaptation at food system level may be additionally needed to counteract air pollution and climate change and their associated possible yield losses, such as by decreasing meat consumption or food waste [195,196]. This suggests that aspects other than farming would define the degree of adaptation of agroecosystems such as willingness of the public to adopt changes in lifestyle. For instance, advanced nitrogen management along with shifts in dietary customs could enhance planetary feeding capacity [197].The complexity in climate change and air pollution lies in the fact that environmental, economic and social dimensions are dynamically linked in both antagonistic and mutually beneficial ways in a system that is highly unpredictable. The systemic approach and combination of disciplinary knowledge in interdisciplinary research enables a multi-perspective view for a closer approximation and better understanding of the phenomena. New approaches are formed in the common exchange process of ideas and perspectives, enabling innovation. However, with underlying differences in research methodology, interdisciplinary collaboration can undoubtedly be challenging, and opinions diverge already at the debate of which knowledge concept is at the forefront [198]. Since the debate over greenhouse gas emissions and the adaptation to climate change, air pollution and other biophysical and social stressors does affect a myriad of stakeholders, the interdisciplinary approach is sometimes found to be insufficient. It has been therefore suggested going beyond an interdisciplinary approach and applying an open transdisciplinary approach, a combination of formal basic knowledge from different disciplines with informal knowledge and application-oriented practical knowledge by linking them in a participatory and adaptive processes [199]. Such inter- and transdisciplinary research is highly needed to adapt crop ecosystems to climate change and air pollution.

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Competing interests

The authors declare that they have no conflict of interest.

Author contributions: E.A., M.F., and Z.F. designed the study. All authors contributed parts of different sections and, thus, all authors contributed to writing the initial draft. E.A., M.F., and Z.F. edited the inititial draft and generated the first draft of the integrated manuscript. All authors revised the paper, read the final manuscript, and approved its submission.

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Figures and captions

Fig. 1. Adaptation of crop production to air pollution and climate change at plant, field, and ecosystem levels. At plant scale, integrating genetic variation, QTL, molecular breeding, and phenotyping can offer a perspective for improving crop performance under such environmental challenges. Then, a number of techniques can be applied on the field, including adjusting cultivation practices (e.g. fertilization, irrigation), diversifying cultivations and promoting mixed cropping systems, applying antiozonants (if toxicologically tested) and biostimulants, utilizing priming technology, and expanding phenotyping-robot-assisted farming. At the ecosystem level, enhancing soil resilience, incorporating remote sensing technology (precision agriculture), and modifying the hydrology and microclimate of agricultural landscapes can further facilitate crop adaptation to climate change and air pollution. Photo sources: Background photo: ©Mokhamad Edliadi (flickr.com; cifor.org); Puzzle pieces: ©Pixabay.com; istockphoto.com.

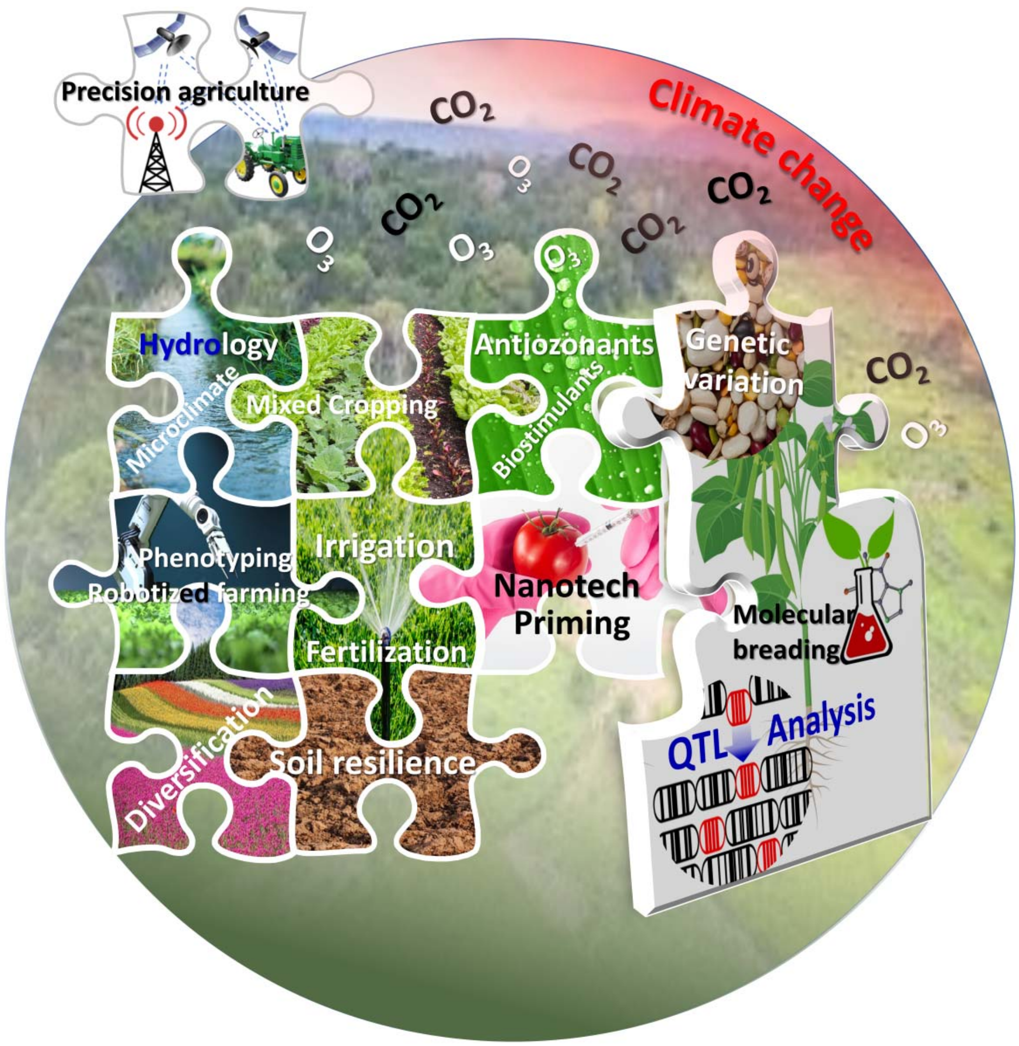
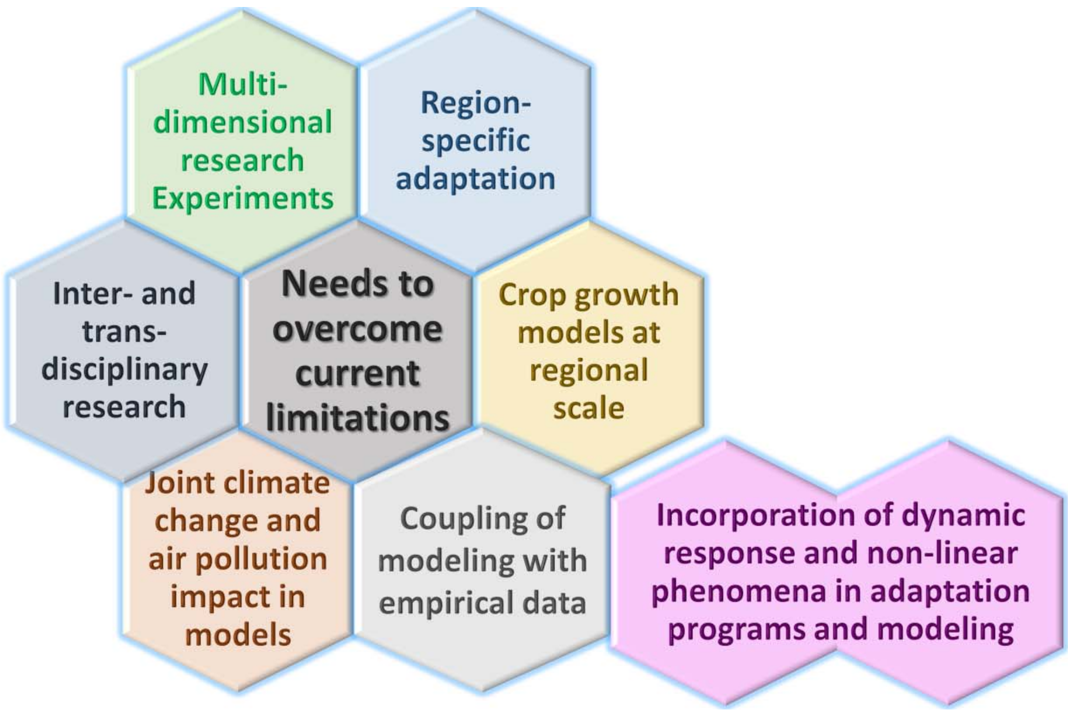
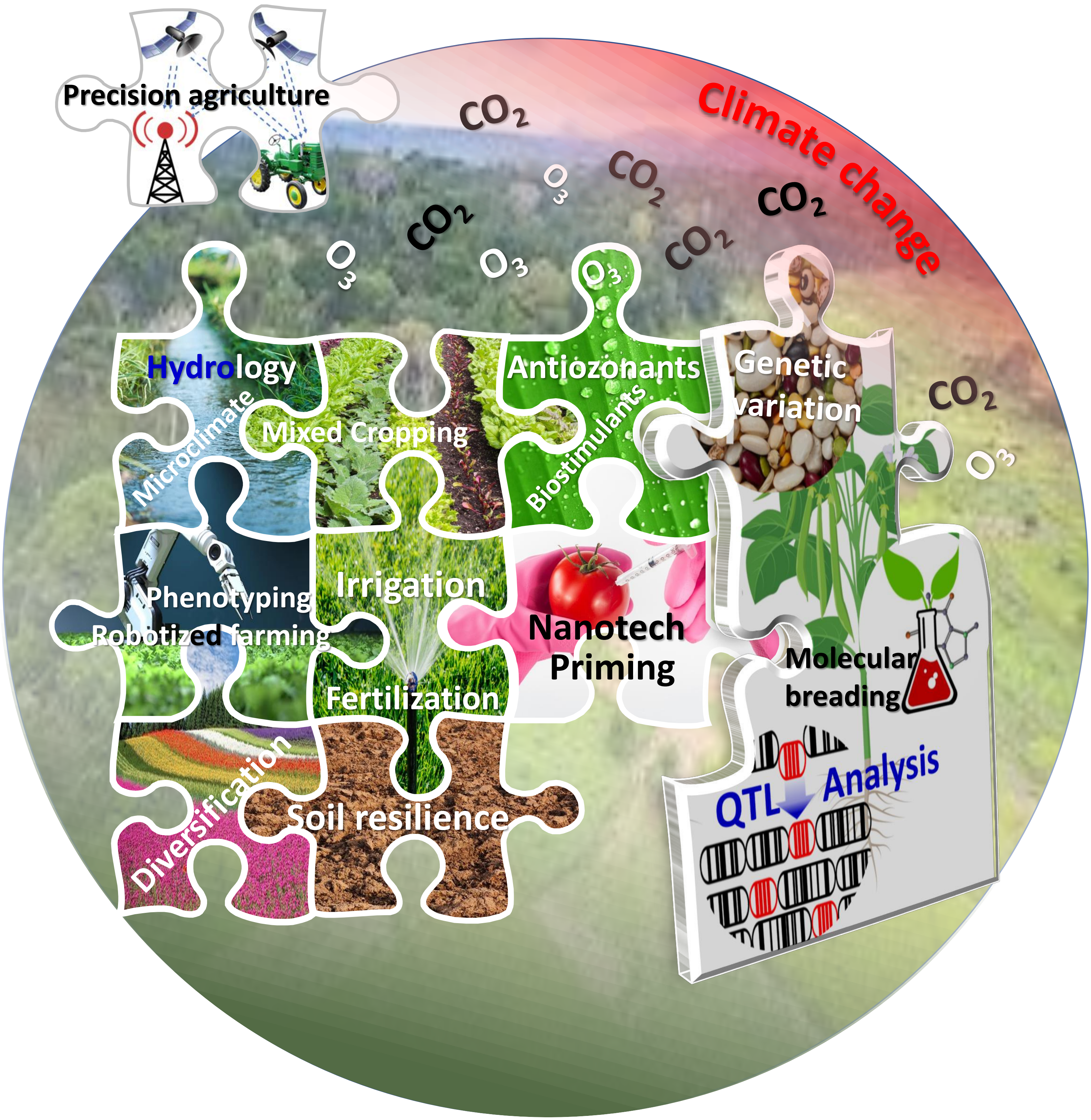
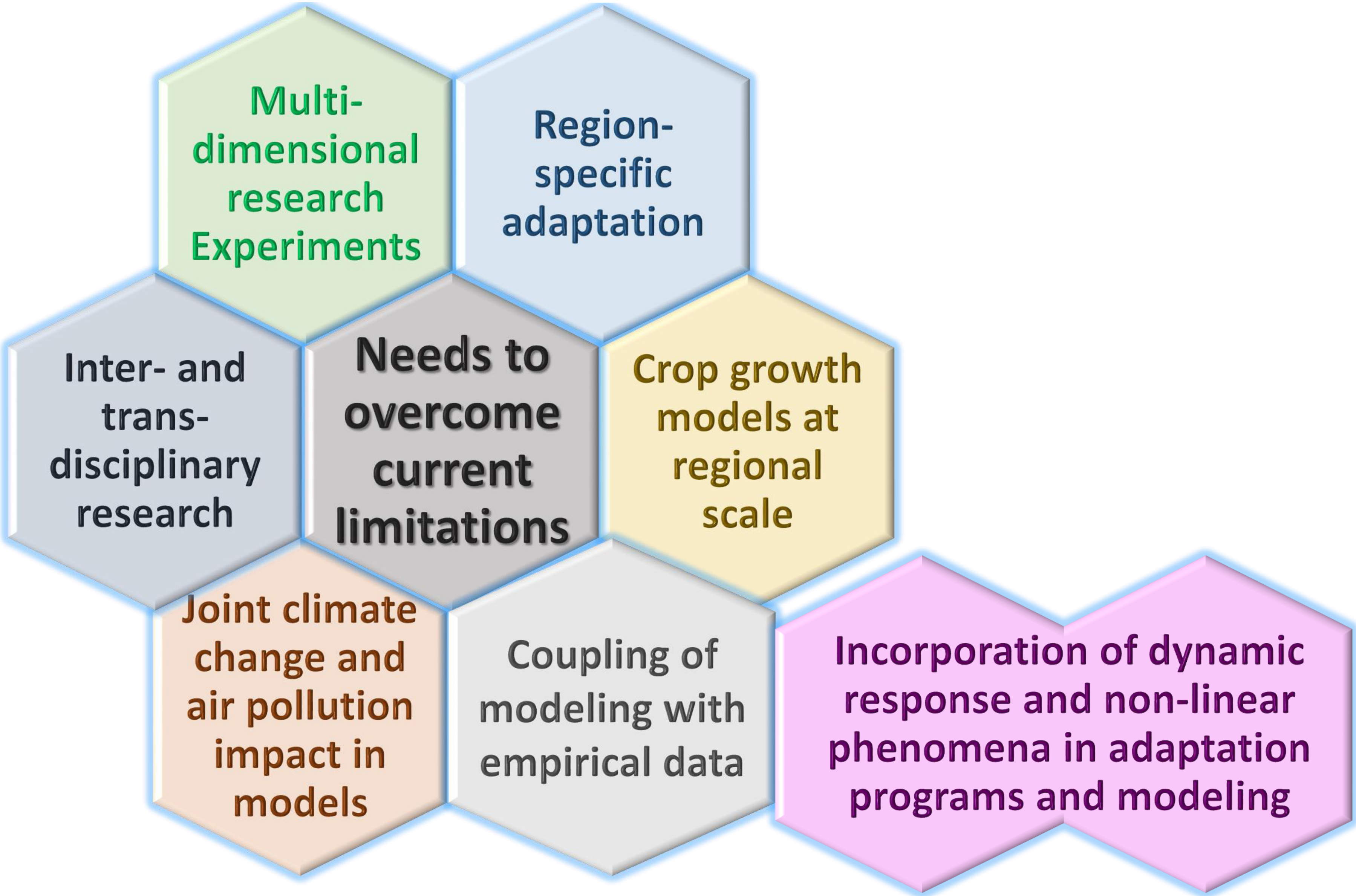


Fig. 2. Overcoming current limitations in adapting agroecosystems to climate change and air pollution at different scales. To overcome current limitations, needs include moving toward more multi-dimensional experiments, employing a transdisciplinary approach, and addressing combined effects of climate change and air pollution in models. Needs also include coupling modeling with empirical data, incorporating pleiotropic responses and non-linear phenomena in modeling and adaptation programs, applying growth models at regional scale, and targeting region-specific adaptation.





Precision agriculture
Climate change
CO_2
O_3
Hydrology
Microclimate
Mixed Cropping
Antiozonants
Biostimulants
Genetic variation
Phenotyping
Robotized farming
Irrigation
Nanotech Priming
Molecular breading
Fertilization
Diversification
Soil resilience
QTL Analysis


Multi-dimensional research Experiments
Region-specific adaptation
Inter- and trans-disciplinary research
Needs to overcome current limitations
Crop growth models at regional scale
Joint climate change and air pollution impact in models
Coupling of modeling with empirical data
Incorporation of dynamic response and non-linear phenomena in adaptation programs and modeling