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# PLANTS AND CLIMATE CHANGE: COMPLEXITIES AND SUPRISES

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**ABSTRACT:**
Anthropogenic climate change (ACC) will influence all aspects of plant biology over coming decades. Many changes in wild species have already been well-documented as a result of increased atmospheric CO2 concentrations, warming climate and changing precipitation regimes. A wealth of available data has allowed the use of meta-analyses to examine plant–climate interactions on more sophisticated levels than before. These analyses have revealed major differences in plant response among groups, e.g. with respect to functional traits, taxonomy, life-history and provenance. Interestingly, these meta-analyses have also exposed unexpected mismatches between theory, experimental, and observational studies. Scope We reviewed the literature on species' responses to ACC, finding 42 % of 4000 species studied globally are plants (primarily terrestrial). We review impacts on phenology, distributions, ecophysiology, regeneration biology, plant–plant and plant–herbivore interactions, and the roles of plasticity and evolution. We focused on apparent deviations from expectation, and highlighted cases where more sophisticated analyses revealed that unexpected changes were, in fact, responses to ACC.

**KEYWORD:** Climate change, global change, phenology, distributions, range shifts, invasive species, assisted colonization, elevated CO2, plant functional groups, plant functional traits, plasticity,

**INTRODUCTION:**

Climate change represents one of the greatest research challenges currently faced by plant biologists, agronomists and conservation biologists. With global greenhouse gas emissions set to continue to rise for the foreseeable future, the impact of elevated atmospheric CO2 (eCO2), and associated shifts in temperature and precipitation are all expected to impact plant ecophysiology, distribution and interactions with other organisms (Intergovernmental Panel on Climate Change (IPCC), 2014). Consequently, effects of anthropogenic climate change (ACC) on plant growth, reproduction, phenology, and distribution have already generated several thousand scientific articles. This wealth of literature has provided fodder for independent global meta-analyses synthesizing data from long-term observational records for some 4000 eukaryote species, about 42 % of which are plants (primarily in terrestrial systems), spread across the world (Table 1). Collectively, these meta-analyses document coherent patterns across the globe of poleward and upward range shifts and advancement of spring phenologies (Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2007; Poloczanska et al., 2013). These results fed into the latest IPCC report leading to the following statement in the Summary for Policy Makers: 'In recent decades, changes in climate have caused impacts on natural and human systems on all continents and across the oceans. Evidence of climate-change impacts is strongest and most comprehensive for natural systems .... Many terrestrial, freshwater, and marine species have shifted their geographic ranges, seasonal activities, migration patterns, abundances, and species interactions in response to ongoing climate change (high confidence).' Summary for Policy Makers (IPCC, 2014) With specific reference to plants, Working Group II of the IPCC (Settele et al., 2014) concluded with 'high confidence' that anthropogenic climate change has had, and will continue to have, a strong effect on plant life cycles and species' interactions. These simple, expected patterns of response to ACC, which have less than one in a billion chance of occurring at random have had crucial input into policy, as witnessed by the Copenhagen Accord drawn up at COP15 which decreed.

This focus on the 'big picture' overall impacts has meant that relatively little research has gone into understanding changes that are counter-intuitive or unexpected as responses to warming climate. Nonetheless, every biological community investigated in detail has contained a minority of species that

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appeared to be showing no response or even changing in a direction counter to expectation from local climate change. This has been true even for communities experiencing strong regional warming. Thus, while there is much that we do know about plant response to climate change, many aspects remain poorly studied, controversial, or simply confusing. This is particularly true for studies on plant population and community ecology where translation of experiments conducted in controlled environments into 'real-world' plant communities has proven to be notoriously difficult. In a recent meta-analysis, Wolkovich et al. (2012) showed that phenological responses to experimental warming treatments failed to match long-term observational responses for many plants, even for the same species growing in the same regions. Most disturbingly, responses not only differed in magnitude, but sometimes differed in direction as well. It is not surprising that plant community responses to climate change in real-world environments are more complex than predictions from relatively simple experiments and models of past decades, but the question remains 'what drives these differences from expectation?'. With these issues in mind, Annals of Botany invited a number of experts to present their research at a sponsored symposium session titled Plants and Climate Change: Complexities and Surprises, held during the 99th Ecological Society of America (ESA) meeting in Sacramento, California, in August 2014. In this special issue, we bring together studies presented at ESA 2014 with additional manuscripts submitted by researchers from around the globe. We highlight ways in which increased ability to interrogate long-term data sets with sophisticated statistical and modelling techniques is generating evidence that many apparently counter-intuitive changes can indeed be understood in the light of climate change after accounting for the true complexity of species' responses and species' interactions. Our aim in this Review article is to set the context for these new studies by summarizing current knowledge and then to suggest how future research might be targeted to better understand observed departures from straightforward expectations. An emergent theme from this synthesis is that in order to better forecast long-term consequences of climate change on plant community structure and function, ecologists must embrace and dissect apparent departures from theoretical predictions, rather than simply assume that a given study 'got it wrong'. We begin with the most data-rich topic—phenological shifts—for which a substantial body of research has shown that advancement of plant growth and flowering has been widely associated with spring warming (Parmesan and Yohe, 2003; Root et al., 2003 , 2005; Parmesan, 2007; Poloczanska et al., 2013). There is also emerging evidence for differences in magnitude of responses across different trophic levels (Parmesan, 2007; Thackeray et al., 2010 ; Poloczanska et al., 2013). As usual, these generalities camouflage individual changes that run counter to the overall trend, and in this case these apparent idiosyncrasies have proven amenable to the 'dissection' approach that we recommend. For example, Cook et al. (2012, summarized in detail below) found that some three-quarters of 'nonresponding' species actually were responding quite strongly to warming seasons, simply in more complex ways than previously recognized. Next , we turn to the second most common topic in climate change impacts, that of changes in species' distributions. The overall message from global meta-analyses of long-term observational datasets indicates that major shifts in species' distributions have already occurred, with some species showing range contractions and others range expansions (Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006; Poloczanska et al., 2013). Species distribution models (SDMs) offer some insights into future biogeographies, but there are still large uncertainties. Both observational and modelling studies point to a series of issues for plant conservation. New challenges include the need for new conservation tools, including controversial approaches such as assisted colonization (Hoegh-Guldberg et al., 2008). Further, as species alter their distributions in attempts to track a shifting climate space, they move into novel geographic areas, opening the possibility for these exotic species to become invasive. Indeed, early concerns about climate change were that existing exotics would benefit over natives and become invasive, and that already invasive species could become even more damaging to native communities and ecosystems (Dukes and

Mooney, 1999). We then discuss what is known about the roles of plasticity and evolution in shaping species' responses to anthropogenic climate change. While recognizing that studies on this issue are still relatively few, there are emerging signs of limited capacity for in-situ adaptive response (Parmesan, 2006). We then turn to some under-studied areas. Experiments on seed and seedling responses are relatively rare, and there is no comprehensive review of these early plant life history stages, although this critical phase often suffers the highest mortality. Although there is a long history of research on the impacts of eCO2 on plant physiology, growth and reproduction (Bolas and Henderson, 1928), few experiments couple CO2 treatments with expected climatic warming and/or shifts in precipitation regimes. Looking more broadly, there is a dearth of studies that incorporate ACC treatments (climate and eCO2) into experiments with other global change drivers (e.g. nutrient addition or land fragmentation). Once again, our need for better mechanistic understanding of plant responses, including physiological and life-history responses, in the context of simultaneous pressure from multiple environmental changes is illuminated by apparent inconsistencies between laboratory and field experiments, and between experimental results and long-term observational data. Finally, we ask what, if anything, can be done to improve our ability to predict which plant species are likely to respond most to 'climate change' in the broadest sense, that is including the direct impact of eCO2 together with indirect effects on plants via changes in temperature and precipitation. More specifically, does incorporation of plant functional traits or functional groupings (based on shared life history traits) into analyses of experiments and long-term observations, as well as into theoretical models, offer any improvement in understanding and predicting plant responses?

**Changing trophic synchrony**

Magnitude of phenological responses differs among trophic levels. In their global meta-analysis of marine systems, Poloczanska et al. (2013) found that predators (fish and zooplankton) had advanced significantly more than their potential food resources (phytoplankton). Similarly, in a meta-analysis of northern hemisphere data, herbivorous insects (butterflies) had advanced at rates three times faster than potential host plants (herbs) (Parmesan, 2007). Likewise, Thackeray et al. (2010) found a trend for UK primary consumers to advance more than producers, though this was not significant. In the same study, secondary consumers had advanced significantly less than all other trophic levels, at about half the rate of the plants and herbivores. These meta-analyses suggest increasing asynchrony between interacting trophic levels (predator–prey and insect– host).

**Future directions in phenological research**

Overall, considerable uncertainty remains about the relative roles of seasonal changes in temperature, precipitation and photoperiod in driving phenological dynamics, thereby hindering our abilities to predict how yearly phenological events may, or may not, shift with changes in climate (Ko¨rner and Basler, 2010). More detailed analyses of geographical variation in plant response may help, and it is clear from Menzel et al. (2006) that strong regional differences exist. This variability opens up the possibilities of comparing responses of different species in different sites that differ in some systematic way (e.g. in resource limitation or other abiotic or biotic environments) that carries an a priori expectation of having specific differences in effects on phenologies under similar climatic change (from theory or empirical studies).

**ROLES OF PLASTICITY AND EVOLUTION IN SHAPING RESPONSES**

A high likelihood of being exposed to novel, potentially stressful conditions is shared by invading exotic species and by populations experiencing climate warming in situ. In both circumstances, plants may respond by a combination of plastic and genetic/epigenetic change. Some authors stress the importance of plasticity (Nicotra et al., 2010), while others protest that evolution is too frequently ignored in predicting responses to climate change (Hoffmann and Sgro, 2011; Anderson et al., 2012). It is clearly important to understand both processes, for the purposes of planning conservation under climate change and for managing productivity of economically important plant populations (des Marais et al., 2013). In recognition of this need, a special issue of Evolutionary Applications, edited by Merila¨ and Hendry (2014), summarizes the relative roles of plasticity and evolution in climate change biology, with one paper (Franks et al., 2014) devoted exclusively to plants. The editors urged better and more standardized methodology to distil the processes involved as natural populations adapt, or fail to adapt, to current climate warming. They also caution against what they regard as a too frequent untested assumption that observed changes, whether plastic or genetic, are indeed adaptive.

**PLANT FUNCTIONAL TRAITS/GROUPING: USEFUL METRICS?**

**Inconsistent messages**

Some authors have advocated using metrics of plant responses based on shared life history characteristics or ecophysiological traits to better understand variation in species' responses to ACC (Lavorel et al., 1997 ; Chapin, 2003; Wullschleger et al., 2014). Plant functional traits (PFTs) or plant functional groups (PFGs) may aid our ability to identify characteristics most likely to exhibit plasticity in the face of environmental change (Nicotra et al., 2010 ; McLean et al., 2014). However, broad groupings based on a vague similarity in growth form often do not offer sufficient resolution to capture important ecophysiological characteristics. There is a need for candidate PFTs to go beyond simplistic comparisons of plant growth forms and instead capture essential ecophysiological characteristics and retain a 'common currency'. Despite 20 years of effort, no clear consensus about what PFTs or PFGs best predict climate response has emerged. In a large synthesis of the literature (29 studies, 6 of which were on plants; mean length of study 58 years), Buckley and Kingsolver (2012) found only a few traits significantly associated with responses, and those were inconsistent across studies. For plant distributions, only one study found a strong association, and that was for species' growth rates to be positively associated with distributional change. Plant phenologies showed a greater number of associated traits, with phylogeny strongly associated with response in two studies, and growth rates and earlier seasonality showing strong association in a third study. Some studies have suggested that 'shrubs' perform relatively well in water-stressed treatments, but closer inspection of the overall trend shows that responses tend to be confined to a limited number of species and/or result from shifts in the performance of one member of a different PFG (Grime et al., 2008; Prieto et al., 2009). Similarly Hanley et al. (2004) showed that while 'forbs' and 'grasses' both exhibited strong responses to $eCO_2$ in chalk grassland microcosms (increasing and decreasing productivity, respectively), these changes were entirely driven by only one species in each group. This seems to be a general trend; Ko¨rner's 2006 review noted that plant community responses to $CO_2$ manipulations were dominated by only a few very responsive species. A meta-analysis by Poorter and Navas (2003) found no variation between 'fast' and 'slow' growing, nor between 'monocot' versus 'dicot' species, in their responses to $eCO_2$. Interestingly, whilePoorter and Navas (2003) found a difference between C3 and C4 plants, this was only seen when soil nutrients were abundant, harking back to the strong effects on interactions among drivers.

**METHODOLOGY:**

Data and facts have been collected from secondary sources for the presented research paper, using various textbooks, newspapers, journals research paper, website etc.

**CNCLUTION:**

We have dealt with only a few of the key issues facing contemporary climate change biology; in addition, myriad interactions between plants and their herbivores, symbionts and competitors are likely to be part, but not all, of the story. It is increasingly clear that variation in plant ecophysiological traits, their inherent adaptability (within and between individuals and entire populations) are vital, but attempts to treat these factors in isolation have confounded our ability to predict how any given species or community will respond to an increase in $CO_2$, temperature, or rainfall. Nonetheless, the complexities of interactions among drivers must be better understood if we are to have any hope of predicting the effects of ACC on biological system.

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