

The Hot and the Classic

GLOBAL WARMING— EFFECTS ON PLANTS

The burning of fossil fuels, the large-scale clearing of forests, and other human activities are altering global climates at an alarming rate. The continued consumption of fossil fuels is expected to result in a doubling of the current $[\text{CO}_2]$ by sometime in this century. These increases in CO_2 as well as other “greenhouse gases” are expected to raise world temperatures by 0.03°C per year in the 21st century. Global warming and increased atmospheric $[\text{CO}_2]$ are already having a major impact on plant distributions. Plants, in general, benefit from slightly warmer temperatures and higher $[\text{CO}_2]$, but not all plants will benefit equally from these conditions, and some may even be harmed: There will be winners and losers in the warmer world of the near future. If the past is any indicator, the losers may greatly outnumber the winners. Palaeobotanical evidence indicates that there was a 4-fold increase in atmospheric $[\text{CO}_2]$ across the Triassic-Jurassic boundary and an associated 3°C to 4°C “greenhouse” warming (McElwain et al., 1999). These environmental conditions were calculated to have raised leaf temperatures above a highly conserved lethal limit, perhaps contributing to the $>95\%$ species-level turnover of Triassic-Jurassic megafloora. Are we destined to witness a floral mass extinction of similar proportions in the coming few centuries? The data and models discussed in this month’s column suggest that the mass extinction, or at least the mass ecological upheaval, has already begun.

Effects on Carbon Metabolism

The climate changes that we are currently undergoing include both increases in temperature and increases in atmospheric $[\text{CO}_2]$. It is well known that C_3 and C_4 plants respond quite differently to temperature and atmospheric $[\text{CO}_2]$. Rising temperatures

will increase the ratio of photorespiratory loss of carbon to photosynthetic gain, whereas rising $[\text{CO}_2]$ will have an opposing effect. All else being equal, C_4 plants tend to be favored over C_3 plants in warm, humid climates; conversely, C_3 plants tend to be favored over C_4 plants in cool climates. Empirical observations supported by a photosynthesis model predict the existence of a climatological crossover temperature above which C_4 species have a carbon gain advantage and below which C_3 species are favored. Model calculations and analysis of current plant distribution suggest that this atmospheric $[\text{CO}_2]$ -dependent crossover temperature is approximated by a mean temperature of 22°C for the warmest month at the current $[\text{CO}_2]$ (Collatz et al., 1998).

In addition to favorable temperatures, C_4 plants require sufficient precipitation during the warm growing season. C_4 plants that are predominantly short stature grasses can be competitively excluded by trees (nearly all C_3 plants)—regardless of the photosynthetic superiority of the C_4 pathway—in regions otherwise favorable for C_4 . Collatz et al. (1998) examined changes in the global abundance of C_4 grasses in the past using plausible estimates for the climates and atmospheric $[\text{CO}_2]$. They predict that global warming during this century will favor C_3 vegetation because the increase in C_3 photosynthetic efficiency that occurs under higher atmospheric $[\text{CO}_2]$ conditions will outweigh the reduction of photosynthesis that is attributable to higher temperatures.

Effects on Phenology

The growth and reproduction of most plants is tightly regulated by the time of season. The phenology or time of flowering of a plant is one such seasonal event that is critical for its sexual reproduction. Although the initiation of flowering is typically mediated by changes in daylength and, as such, is independent of temperature, the time required for flowers to develop to maturity, like most growth processes, is strongly dependent upon temperature. Many recent reports in-

dicating the time of first flowering has been affected by the warming trend of the last half century. For example, Abu-Asab et al. (2001) found that the trend of average first-flowering times per year for a group of 100 plant species growing near Washington, DC, have shown a significant advance of 2.4 d over the past 30 years. When 11 species that exhibit later first-flowering times were excluded from the data set, the remaining 89 show a significant advance of 4.5 d on average (ranging from -3.2 to -46 d). The advances of first flowering in these 89 species were directly correlated with local increases in minimum temperature. The average temperature during the month or so preceding flower opening appears to be largely responsible for causing the advances of first-flowering times.

A more recent report by Fitter and Fitter (2002) has revealed just how rapidly these changes in flowering time are occurring. These researchers found that the average first flowering date of 385 British plant species has advanced by 4.5 d during the past decade compared with the previous four decades. Sixteen percent of species flowered significantly earlier in the 1990s than previously, with an average advancement of 15 d in a decade. The authors also found that different types of plants responded to varying degrees. For example, annuals were more likely to flower earlier than perennials, and insect-pollinated species more than wind-pollinated. Accelerated phenologies may alter patterns of resource allocation, may affect interactions with pollinators, and could alter the size, species richness, and intraspecific genetic diversity of the soil seed bank.

Massive Ecological Upheavals

The distribution of many species tends to be limited to a narrow range of environmental conditions. One of the consequences of the increased growth seasons and earlier flowering times afforded by global warming will be that the natural ranges of many plant species will shift polewards. For

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example, Iverson and Prasad (1998) developed models to evaluate potential shifts for 80 individual tree species in the eastern United States. They concluded that roughly 30 species could expand their range while an additional 30 species could decrease by at least 10%, following equilibrium after a changed climate. Depending on the global change scenario used, four to nine species would potentially move out of the United States to the north. Nearly half of the species assessed (36 out of 80) showed the potential for the ecological optima to shift at least 100 km to the north, including seven that could move >250 km. Actual species redistributions, however, may be controlled by migration routes through fragmented landscapes.

There is already ample empirical evidence that many plant species are beginning to invade formerly colder climes as the world's temperature has begun to rise. For example, researchers in Alaska combed through archives of aerial photos, comparing those of the same locations taken 50 years ago. Of the 66 aerial photos included in the study, growth increases were reported in over half (Sturm et al., 2001). In the Swedish Scandes since the early 1950s, the range-margins of mountain birch (*Betula pubescens*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), rowan (*Sorbus aucuparia*), and willows (*Salix* spp.) have advanced by 120 to 375 m to colonize moderate snow-bed communities (Kullman, 2002). Ring counting of a subsample of these saplings revealed that, with one exception, they were aged between 7 and 12 years, i.e. they germinated after 1987. Another example is afforded by the replacement of macrolichens by invading vascular plants in the climatically milder parts of the Arctic (Cornelissen et al., 2001). These macrolichens are critical for the functioning and biodiversity of cold northern ecosystems and their reindeer-based cultures.

In some cases, however, there may not be enough intraspecific variation, phenotypic plasticity, or continuity in landscape to help certain plant species

to cope with the sudden climate changes. For example, Etterson and Shaw (2001) characterized the genetic architecture of three populations of a native North American prairie plant in field conditions that simulate the warmer and more CO₂-rich climates predicted by global climate models. The predicted rates of evolutionary response were much slower than the predicted rate of climate change. The local extinction of such species seems a likely outcome.

Changes in Food Web Structures

Of course, plants do not exist in isolation but interact with other organisms (e.g. pollinators, competitors, mycorrhizae, pathogens, and herbivores). These organisms, too, will be affected by global warming in their own ways. As such, it is virtually impossible to predict with any certainty how any given species will succeed in the face of global warming). One approach to this question is the use of artificial microcosms (Petchey et al., 1999). Microcosms permit experimental control over species composition and rates of environmental change. Petchey et al. (1999) concluded based on such microcosm experiments that extinction risk in warming environments depends on trophic position. Warmed communities disproportionately lost top predators and herbivores and became increasingly dominated by autotrophs and bacteriovores. Changes in the relative distribution of organisms among trophically defined functional groups led to differences in ecosystem function beyond those expected from temperature-dependent physiological rates. Diverse communities retain more species than depauperate ones, which suggests that high biodiversity buffers against the effects of environmental variation because tolerant species are more likely to be found. Studies of single trophic levels clearly show that warming can affect the distribution and abundance of species,

but complex responses generated in entire food webs greatly complicate predictions.

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