



Review

Overwintering of herbaceous plants in a changing climate. Still more questions than answers



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ABSTRACT

The increase in surface temperature of the Earth indicates a lower risk of exposure for temperate grassland and crop to extremely low temperatures. However, the risk of low winter survival rate, especially in higher latitudes may not be smaller, due to complex interactions among different environmental factors. For example, the frequency, degree and length of extreme winter warming events, leading to snowmelt during winter increased, affecting the risks of anoxia, ice encasement and freezing of plants not covered with snow. Future climate projections suggest that cold acclimation will occur later in autumn, under shorter photoperiod and lower light intensity, which may affect the energy partitioning between the elongation growth, accumulation of organic reserves and cold acclimation. Rising CO₂ levels may also disturb the cold acclimation process. Predicting problems with winter pathogens is also very complex, because climate change may greatly influence the pathogen population and because the plant resistance to these pathogens is increased by cold acclimation. All these factors, often with contradictory effects on winter survival, make plant overwintering viability under future climates an open question. Close cooperation between climatologists, ecologists, plant physiologists, geneticists and plant breeders is strongly required to predict and prevent possible problems.

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Abbreviations: IPCC, The Intergovernmental Panel on Climate Change; RCPs, Representative Concentration Pathways.

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1. Introduction

The average temperature of the Earth surface has increased by 0.85°C since 1880, largely as a result of human activity, mainly the production of greenhouse gases [1]. It is predicted that even if greenhouse gas emissions could be fixed at the current level, the temperature would continue to rise before it eventually starts to fall again. The Intergovernmental Panel on Climate Change (IPCC) mentions four Representative Concentration Pathways (RCPs) in its fifth assessment report. They describe four possible climate future scenarios. RCP2.6, RCP4.5, RCP6.0, and RCP8.5, are named after a possible range of radiative forcing values ($+2.6$, $+4.5$, $+6.0$, and $+8.5\text{ W m}^{-2}$, respectively) in the year 2100. RCP2.6 represents a very optimistic pathway with stringent climate policies to limit emissions, whereas RCP6.0 and RCP8.5 represent more pessimistic pathways with limited or not climate policies. According to these RCPs, the average global surface temperature is expected to rise by 1.0°C , 1.8°C , 2.2°C and 3.7°C , respectively between 1986–2005 and 2081–2100. The models were run with an assumption of CO_2 concentrations reaching 421 ppm, 538 ppm, 670 ppm, and 936 ppm, respectively, by the year 2100 [1].

Greater temperature increases are predicted at higher latitudes and in winter, rather than in summer [1]. Moreover, the daily and seasonal minimum temperature is predicted to increase more than the maximum temperatures [1]. All in all, this would suggest a decreased risk of exposure to extreme low temperatures for temperate grassland and crop in the future. However, the frequency, degree, and length of extreme winter warming events, leading to partial or complete snowmelt during winter, increased during the last 50-years [2,3]. If this situation persists, plants may be at a greater risk of frost-induced damage due to lack of snow cover, and of anoxia damage due to accumulation of ground ice. Snow cover is a good insulation, and a 10–20 cm layer is often enough to smooth outmost of the fluctuations in air temperature and maintain the temperature around the plant is close to the freezing [4], except for areas with more extreme low temperatures, where a 30–40 cm layer of snow is needed [5]. As global warming will decrease both the duration of snow cover and snow depth [1], resulting in plants being exposed to freezing temperatures in the future due to decreased snow cover. This can only be assessed locally through a comparison of air temperature fluctuations and snow cover data in the climate change projections [4]. Historical observations indicate that the land area covered by snow in spring in the Northern hemisphere has decreased by 7% since 1922. Projections of spring snow covered land area for the Northern hemisphere by the end of the 21st century predict a further decrease between 7% (RCP2.6) and 25% (RCP8.5) [1]. Regional projections for 2100, compared with current conditions in Norway, indicate quicker snowmelt by up to 2–3 months for low-land regions and up to 1 month for high-altitude regions [6]. For eastern Canada, a decrease in the duration of snow cover by 1.5 month is expected within the next 50 years [7]. For the Swiss Alps, it has been predicted that the snow line would move 150 m up for each increase of 1°C .

The increased winter temperatures will be generally accompanied by increased precipitation in autumn and winter at higher latitudes [1]. This will change the risk of water-logging, snow and ice accumulation on the fields. Moreover, the amount of light that is already low due to the sun inclination in this period, will be further reduced because of increased cloud cover. For example, the greater winter precipitation will result in an increase in seasonal maximum snow depth at high-altitude locations in Norway, but not in low-land locations, where much of the precipitation will fall as rain [6]. On a larger scale, increases in maximum monthly snow depths are expected for Siberia and northern Canada, while decreases are expected for most other regions of the Northern hemisphere [1]. Extreme precipitation events are likely to become more intense

and more frequent by the end of the 21st century for mid-latitude land areas, and likely for most land areas at other latitudes [1].

While it is well established that the average temperature has increased over the last century and will continue to rise even in the most optimistic RCP, there is still large uncertainty concerning the temperature variability within a given year and between years [1]. With the perspective of winter survival, the day-to-day variation is of special interest. A common misconception among biologists and agronomists, concerned with plant winter survival in the future, seems to be the assumption that the global warming will lead to an increased frequency of freezing and thawing cycles. Temporary increases of such cycles may occur at locations going through a transition from winters with stable sub-zero temperatures to milder conditions [8], such as for many locations in continental Canada [9]. Still, the general trend seems to be a decrease in the frequency of freezing-thawing cycles, as shown for example in the regional down-scaling studies for Norway [6] and in statistical modeling studies for Germany [10]. Several studies have also indicated a trend of reduced day-to-day temperature variability in the winter season during the last 50–100 years [11,12]. Furthermore, a brief analysis of daily temperature extremes described in the Fifth Coupled Model Intercomparison project also suggests that there will be a decrease in the intra-seasonal variability of European winter temperatures [13]. However, it should be noted that the occurrence of cold extremes is dependent on a number of factors that the current climate models cannot predict with great confidence, such as blocking events and atmospheric flow of cold air to warmer regions [8]. Given the large uncertainty concerning future winter temperature variability, biologists should neither overemphasize nor exclude the possibility of increased variability.

2. Simulation models for understanding climate change impact on the vegetation

Simulation models are necessary tools for understanding climate changes and their impact on the vegetation, including the performance of agricultural crops. Several process-based models are available that simulate the yield-building processes in grasslands. Each model has a unique representation of plant processes in the form of mathematical functions. Examples of the models available for temperate grasslands include LINGRA, CATIMO, PaSIM or STICS. Several of these models have been used to simulate the impact of climate change on the yields of grassland in temperate regions. Most simulation studies indicate increased annual grass yields at high latitudes, where temperature is the major growth limiting factor [14–16], and decreased grass yields in many regions at lower latitudes, where growth is predicted to become increasingly limited by water availability [17]. All these studies are limited due to being carried out with models that do not account for the possible effect of climate change on the winter survival of grasses. No model yet available simulates the effect of the major winter stress factors on the winter survival of grasslands. There are, however, models available for other crops [18,19], including perennial grasses [20], that simulate freezing tolerance as a function of air temperature around a plant and plant development stage which can be used for the assessment of frost injury risk under different climate conditions.

The impact of climate change on cold hardening in the autumn and of risk of frost and ice related damage during winter was assessed using the freezing tolerance model in timothy and perennial ryegrass [20]. This was later followed by a similar study for a larger region in the Northern Europe [15]. Simulations of the future conditions (2040–2065) were compared with the baseline period of 1960–1990. The simulations indicated that the risk of frost and ice related injury would remain low at the most locations in the

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