

Review

Optimal Regulation of the Balance between Productivity and Overwintering of Perennial Grasses in a Warmer Climate

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Abstract: Seasonal growth patterns of perennial plants are linked to patterns of acclimation and de-acclimation to seasonal stresses. The timing of cold acclimation (development of freezing resistance) and leaf growth cessation in autumn, and the timing of de-acclimation and leaf regrowth in spring, is regulated by seasonal cues in the environment, mainly temperature and light factors. Warming will lead to new combinations of these cues in autumn and spring. Extended thermal growing seasons offer a possibility for obtaining increased yields of perennial grasses at high latitudes. Increased productivity in the autumn may not be possible in all high latitude regions due to the need for light during cold acclimation and the need for accumulating a carbohydrate storage prior to winter. There is more potential for increased yields in spring due to the availability of light, but higher probability of freezing events in earlier springs would necessitate a delay of de-acclimation, or an ability to rapidly re-acclimate. In order to optimize the balance between productivity and overwintering in the future, the regulation of growth and acclimation processes may have to be modified. Here, the current knowledge on the coordinated regulation of growth and freezing resistance in perennial grasses is reviewed.

Keywords: CBF; climate change; cold acclimation; de-acclimation; freezing; growth; light; photoperiod; seasonality; stress; temperature; winter survival

1. Introduction

Changes in atmospheric CO₂ concentration, temperature, and precipitation patterns are expected to affect plant productivity in a complex manner due to a set of mechanisms and interactions at different scales from leaf to agro-ecosystem [1]. In regions or periods where water availability is sufficient, elevated atmospheric CO₂ concentrations and higher temperatures can potentially increase growth rates of many plant species, including C₃ grasses and forage legumes, and thus increase grassland productivity [2]. In addition to this direct effect of temperature and CO₂ concentration, cool regions with non-productive winters are likely to have longer thermal growing seasons (often defined as the part of the year when the daily mean temperature exceeds 5 °C), with earlier springs and later autumns. For example, in Finland, where the annual mean temperature has most likely increased by at least 2 °C during the last 150 years [3], the thermal growing season was predicted to become one to three months longer by the end of the century as compared to the period 1971–2000 [4]. Such extended growing seasons are expected to contribute to the increase in annual grassland yields in temperate climates [5–9]. Although the prediction models used so far account for drought limitations on growth, they do not account for possible effects of plant survival during seasonal stresses. However, a recently developed model, which incorporates both the cold acclimation process in autumn and winter survival, will improve predictions for high latitudes in this respect [10].

Perennial grasses have the potential to utilize the light energy over a larger part of the year than most annual crops, but should survive and produce biomass for several years. The annual recurrent periods of winter stresses or summer droughts in some regions have led to the evolution of seasonal acclimation and de-acclimation processes regulating the level of resistance to seasonal stresses [11–13]. These processes, which are largely regulated by temperature and photoperiod, correlate with changes in growth, development, and dormancy status [13–15], and latitudinal clines in growth responses to temperature and photoperiod have been described [16]. Acclimation and de-acclimation are associated with cessation and resumption of leaf growth, respectively, suggesting a classical growth–stress survival trade-off [17] in the adaptation to seasonal stresses [15]. It is important to note, though, that cessation of leaf growth does not always mean cessation of biomass accumulation, but rather a shift in allocation of photosynthates from leaf blades to newly formed tillers, roots, and storage tissues [18]. Although some perennial grasses have been shown to possess summer endodormancy of shoot meristems [12,14], the existence of winter endodormancy has not been demonstrated to my knowledge, although perennial grasses are obviously ecodormant during cold winter periods. Instead, the shoot meristems that are formed during the latter part of summer and/or during autumn (variations between species) are more or less unresponsive to long day-induction of reproductive development. They gradually become responsive during weeks of low temperature (vernalization), a process which occurs faster in short than in long photoperiods [19].

Winter survival of perennial grasses can be measured directly at the individual plant level, but is frequently measured at sward level as the relative recovery in spring, a measure which also encompasses rate of tiller survival, and earliness and rate of regrowth. Winter survival is an extremely complex trait being the result of both an acclimation process and responses to numerous types of stresses that plants encounter and must endure during winter and early spring [20]. The term “cold acclimation” refers to the development of resistance to freezing stress. Temperature is a major environmental factor controlling cold acclimation and cold de-acclimation in perennial grasses, although light factors are also of importance. Low temperature induces not only freezing resistance, but also resistance to other winter stresses, such as ice encasement/anoxia [21], and fungal pathogens (snow molds) [22,23], which, depending on climatic conditions, may have a much stronger influence on winter survival than freezing [20].

Temperatures are increasing in most regions of the world [24,25], but the annual variation in photoperiod will remain the same. We will therefore have new seasonal combinations of temperature and photoperiod in the future, particularly at high latitudes, where photoperiod changes dramatically during the course of a year. This may lead to mismatches between annual cycles of growth, development, and stress resistance. In order to utilize the new seasonal patterns to maximize the production of biomass from perennial grasses, while maintaining sufficient survival through stressful parts of the year, we need species and varieties with temperature and photoperiod responses conferring an annual growth pattern that optimizes the balance between growth and survival. This review aims to describe the physiological and genetic factors that determine the balance between the productivity and overwintering of perennial grasses in the longer thermal growing seasons expected at high latitudes in the future.

2. Can We Increase Autumn Productivity at High Latitudes?

Autumn-extended thermal growing seasons, combined with higher atmospheric CO₂ concentrations, have the potential to increase the productivity of perennial grasses in the autumn [6–9]. However, since the annual variation in temperature lags behind the annual variation in photoperiod, there is less light in autumn than at comparable temperatures in spring (Figure 1). Therefore, light availability may limit the utilization of the extended growing season in autumn [26,27]. Insufficient light not only limits growth rates, but can also prevent proper acclimation to several types of winter stress [28–33]. Light factors during the cold acclimation period can affect the freezing tolerance of herbaceous overwintering plants in several ways [34,35]. Firstly, a certain irradiance combined

with low temperature increases photosystem II (PSII) excitation pressure, which is a signal leading to the development of freezing resistance [36–40]. Secondly, short photoperiod and low red to far red light (R:FR) ratio can interact with low temperature to stimulate the development of freezing resistance [41–44]. Thirdly, irradiance is the energy source for the accumulation of carbohydrates with a functional role in freezing resistance [40]. In addition, irradiance is the energy source for the accumulation of carbohydrate reserves needed for maintenance and stress responses during winter, as well as for early regrowth in spring.

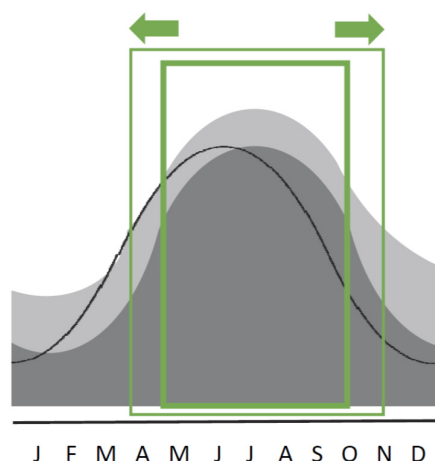


Figure 1. The thermal growing season and annual variation in photoperiod and temperature at a northern latitude. With higher temperatures in the future (light grey area), the thermal growing season will extend in both ends (outer green box) as compared to today (dark grey area and inner green box). The annual changes in temperature (grey area) lags behind the annual changes in photoperiod (black line). With higher temperatures in the future, but the same photoperiod variation as today, we will have new combinations of temperature and photoperiod.

In order to obtain high productivity over several years, a high rate of winter survival and vigorous spring regrowth is necessary, and therefore increased autumn productivity through an extended growing season can only be sustainably achieved if there is enough light during the delayed cold acclimation period. The required levels of acclimation and of stored carbohydrate reserves depend on the severity of the prevailing stresses and on the magnitude of the net photosynthetic deficit that might accumulate during winter, both which can vary greatly from year to year, and which do not necessarily diminish with climate change [20]. There are, in theory, two contrasting options for genetic adaptation to autumn-extended thermal growing seasons at high latitudes: either utilize the extended growing period and cold acclimate later in the autumn, but at the same temperature as today, or cease leaf growth and cold acclimate at the same photoperiod as today, but at higher temperatures (Figure 2). Which option is the best one with regard to optimization of long-term yield would depend on the amount of light needed for sufficient cold acclimation and for sufficient accumulation of carbohydrates. The relative importance of temperature and light factors in cold acclimation and cessation of leaf growth in perennial grasses is not very well characterized, neither are the interactions between temperature and light. It has been suggested that plants adapted to the extreme north rely more on photoperiod than temperature for timing of cold acclimation and cessation of leaf growth than other plants, and that such photoperiodic control will be of increasing importance in southern Scandinavia in the future [32]. The genetic association between cold acclimation and cessation of leaf growth is also not well characterized. The negative correlation between accumulation of carbohydrate reserves and production of harvestable biomass (i.e., assimilate partitioning) is difficult to get around. The association between leaf growth and cold acclimation may have a regulatory cause (discussed

below) rather than a physiological cause, and thus it may be possible to break this association through breeding, as has been suggested for alfalfa (*Medicago sativa* L.) [45–47].

When considering the possibilities for adaptation to autumn-extended thermal growing seasons, it would be relevant to know: (1) to what extent do perennial grasses depend on PSII excitation pressure for induction of cold acclimation and how much light is required for this? (2) how much carbohydrate reserves are needed, and how much light is required after cessation of leaf growth, if any, to build this storage? and (3) how are the different aspects of growth, allocation of photosynthates, and cold acclimation regulated by environmental and genetic factors?

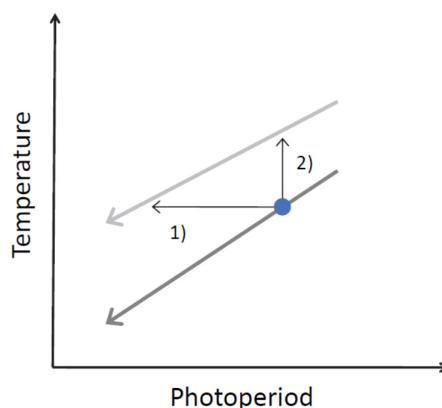


Figure 2. What is the optimal timing of cold acclimation and cessation of leaf growth in autumn? The grey arrows indicate the change in photoperiod and temperature during current (dark grey) and future (light grey) autumns. The timing of cold acclimation and cessation of leaf growth (blue dot) in the future climate could occur (1) at the same temperature as today, but shorter photoperiods (horizontal black arrow), or (2) at the same photoperiod as today, but warmer temperatures (vertical black arrow). Option (1) would allow higher biomass production, but cold acclimation and accumulation of sufficient carbohydrate reserves might be compromised by limited light energy.

2.1. The Role of Light in Signalling Mechanisms Inducing Cold Acclimation

Low temperature limits the rates of enzymatic reactions of photosynthesis more than the rates of electron transfer reactions in the light harvesting systems. As a result, low temperature in light creates an energy imbalance in the photosystems, leading to a change in the redox state of photosynthetic electron-transport components and a high excitation pressure of PSII [36–38]. The altered photosystem redox state functions as an irradiance-dependent cold sensor. As a result of the PSII over-excitation, reactive oxygen species (ROS) are generated, and these may act in signaling pathways leading to the expression of genes involved in freezing resistance [48,49] as well as a compact growth habit in overwintering herbaceous plants [36,37,50–53]. This mechanism of sensing cold might become less efficient if the cold acclimation period is shifted to a later time in autumn in the future, particularly at high latitudes, where irradiance levels are rapidly declining during that time of year. There are, however, also other mechanisms by which plants may sense low temperature and initiate development of freezing resistance, such as changes in membrane rigidity, temperature-dependent histone-DNA interactions, and conformational changes of RNA and protein structure [48,54]. These mechanisms may increase in importance if the cold acclimation period is postponed to a later time of year in the future.

Overwintering plant species have different strategies to handle the potentially damaging excess energy associated with elevated PSII excitation pressure [37–39]. In winter wheat and winter rye the photosynthetic capacity is upregulated during cold acclimation (photochemical quenching, q_p), ensuring utilization of the energy available from the light harvesting complexes. Compared to winter cereals, spring cereals exhibit less photosynthetic acclimation, rely more on dissipation of

excess energy by release of heat (non-photochemical quenching, NPQ) and less on q_p , and are more sensitive to both photoinhibition and freezing [55–57]. In the perennial grasses meadow fescue (*Schedonorus pratensis* Huds., syn. *Festuca pratensis* Huds.), perennial ryegrass (*Lolium perenne* L.), and timothy (*Phleum pratense* L.), NPQ appears to be a more important mechanism of photosynthetic acclimation to cold than q_p [58–60]. In the less freezing resistant Italian ryegrass (*L. multiflorum* L.), q_p increased after cold acclimation and NPQ decreased, while a part of meadow fescue chromosome 4 introgressed into Italian ryegrass was associated with higher cold-induced NPQ and freezing resistance [59]. However, it appears that both NPQ and q_p take place and that the relative importance of these two mechanisms vary among genotypes. For example, Kosmala et al. [61] found higher amounts of some proteins involved in photosynthetic carbon metabolism in a freezing resistant genotype of meadow fescue than a less tolerant genotype, suggesting a role of q_p . Moreover, the relative magnitudes of NPQ and q_p may be related to the carbohydrate status of the plant, with higher q_p in plants with less stored carbohydrates. Selection of photochemical quenching rather than non-photochemical quenching as a mode of photoacclimation to cold appears to be favorable as some of the accumulating photosynthates could either support survival during a long winter or be converted into forage production the following spring.

2.2. The Role of Photosynthates in Winter Survival

In temperate perennial grasses, simple carbohydrates accumulate during cold acclimation and most of these are converted into fructans, which accumulate mainly in the basal part of the shoot [18,62,63]. In regions with a long winter, a storage of organic reserves, particularly carbohydrates, are necessary for maintenance respiration, stress responses, and early spring regrowth. In addition, carbohydrates have specific roles as osmolytes and protectants of cellular components [13,40], and winter survival ability is often associated with a higher concentration of both simple sugars and fructans in the basal parts of the shoot attained during cold acclimation [64–67]. As described above, winter cereals maintain CO₂-fixation rates at low temperatures due to photosynthetic acclimation, a mechanism, which combined with restrictions on leaf growth, ensures that a storage of carbohydrates is accumulating. Elevated atmospheric CO₂ concentrations may affect cold acclimation and winter survival in several ways. For example, higher CO₂ concentrations could inhibit the generation of a PSII excitation pressure signal or enhance the accumulation of carbohydrate reserves. The few studies of perennial grasses have contrasting results regarding the impact of elevated CO₂ on freezing resistance [30,68,69].

The amount of carbohydrate reserves that have to be stored in order to ensure winter survival depends on several factors. A general assessment is that a larger carbohydrate storage will be required in areas where photosynthesis is limited for a long period due to low irradiance, thick snow cover, freezing temperatures, or dying leaf blade tissues, meaning that the plants must draw on stored reserves. Obtaining as high annual yields as possible while maintaining tiller survival is a fine-tuned balance between the allocation of autumn photosynthates into leaf growth versus storage. The potential for utilizing light energy in longer growing seasons (beyond the autumn equinox) for increased autumn yield, rather than for storage, may therefore be highest at lower latitudes and diminish as we move towards higher latitudes with darker autumns and longer winters. Interestingly, during a relatively mild winter without snow cover (approximate average temperature 2 °C) at 61° latitude in western Norway, timothy and perennial ryegrass both accumulated carbohydrates in the shoot base during winter, and more so in the most winter hardy species/cultivars [62,70]. Although this could be due to reallocation within the plant, it is known that photosynthesis can operate at very low temperatures around or even below 0 °C [71,72]. This result indicates that at this latitude, there may be possibilities for maintaining or even accumulating a carbohydrate storage during such mild winters. It is, however, a prerequisite that the leaf tissue survives, and it is likely that there will be strong effects of the timing of the last defoliation, as the amount of new leaf area developed prior to the cessation of leaf growth is critical. Predictions of ideotypes for different regions in a future climate [73] could aid breeding efforts

to achieve the optimum balance between allocation of photosynthates to leaf growth versus storage. The severity of winter conditions vary greatly from year to year, and plants need to be designed to be able to survive winters that are harsher than the average winter. In any case, when it comes to photosynthates, these are possibly better invested in rapid regrowth in spring, when light conditions are very good, than in autumn growth.

2.3. Regulation of Leaf Growth versus Cold Acclimation

In herbaceous overwintering plants, leaf growth inhibition in response to low temperature is not simply a result of lower metabolic rates, but an actively regulated process, which is coordinated with changes in carbon metabolism [74]. Concomitantly with the development of freezing resistance at low temperatures, winter rye, winter wheat, *Arabidopsis thaliana*, and *Brassica napus* develop a dwarf phenotype with shorter, thicker leaves that have a distinct anatomy and high concentrations of proteins and carbohydrates [75]. In addition, these species upregulate their photosynthetic capacity to compensate for the slower rates of enzymatic reactions at low temperature, and accumulate carbohydrates in storage organs. Unlike winter cereals, spring cereals do not develop a dwarf phenotype during cold acclimation, do not upregulate the photosynthetic capacity to the same level, and are not able to attain the same level of freezing resistance [57,75].

In experiments with several perennial forage grasses exposed to different photoperiods, but the same total amount of photosynthetic active radiation (PAR), it was shown that long photoperiods stimulate increased specific leaf area (SLA, leaf area per unit of leaf dry weight) and increased dry matter production, and conversely, that short photoperiods result in lower SLA and productivity [76–78]. Short photoperiod also stimulates tiller formation in perennial forage grasses [79,80], a process which likely improves the potential for spring productivity. Interestingly, at short photoperiods, low irradiance levels, and relatively high autumn temperatures (12 °C), a stimulation of leaf elongation was observed in perennial ryegrass and timothy [33], indicating that when the temperature is not low enough, the shade avoidance syndrome [81] can override the photoperiod response of leaf elongation. This could possibly become a problem during mild, rainy autumns at high latitudes in the future.

C-REPEAT BINDING FACTORS (CBFs) appear to be central in the coordinated regulation of leaf growth and freezing tolerance in response to low temperature [34,74] (Figure 3). CBF transcription factors upregulate whole sets of genes encoding proteins with direct functions in freezing resistance [82]. Temperate grasses have a large number of CBF genes, which are differentially expressed in response to various environmental signals [82–88]. Exactly which of the CBF genes has the largest influence on freezing resistance appears to vary between species, genetic background, and/or environment [89–92]. One of the three CBFs in *A. thaliana* is upregulated by PSII excitation pressure, redox state of the plastoquinon pool, and ROS signaling [49]. However, barley mutants with an impaired chloroplast development had normal cold-induced expression of at least some CBFs, indicating that their expression does not depend solely on a signal generated in the chloroplasts [93]. Indeed, Marozsán-Tóth et al. [85] showed that some CBFs in barley were regulated through Ca²⁺ signaling. Short photoperiods and low R:FR ratios can interact with temperature to induce freezing resistance in *A. thaliana*, and this effect is mediated by the circadian clock through its control of CBF expression [42,43]. In wheat and barley, low R:FR ratios upregulate expression of CBF14 as well as freezing resistance [44], and in meadow fescue CBF6 expression is affected by interactions between temperature, light quality, and irradiance [94]. In *A. thaliana*, CBFs can down-regulate leaf growth by down-regulating the content of gibberellic acid (GA), thereby allowing the accumulation of DELLA proteins which inhibits growth, and in addition increases freezing resistance by a reduction of ROS [95,96]. CBFs can also enhance photosynthetic capacity in *B. napus* [56,97,98], and may therefore play a role in photosynthetic quenching and maintenance of biomass accumulation at low temperatures. All this points to the CBF family of transcription factors as integrators of many different adaptive responses to autumn conditions leading to winter survival.

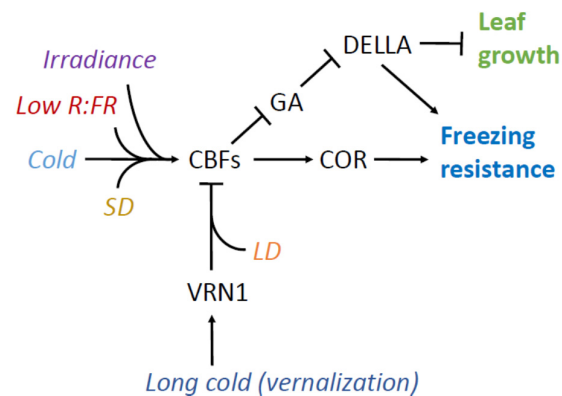


Figure 3. Putative model showing the central role of CBF transcription factors in coordinating freezing resistance and leaf growth in response to temperature and light. Cold induces expression of *CBFs*, which are important in the development of freezing resistance through the induction of the CBF regulon of cold-induced genes (here collectively indicated with *COR*), and also play a role in down-regulation leaf growth via gibberellic acid (GA). Short days (SD), irradiance, and low red to far red light-ratio (R:FR), can take part in the induction of *CBFs*. Prolonged cold leads to a gradual increase in *VRN1* transcripts. *VRN1* can down-regulate *CBFs* and freezing resistance, particularly in long days (LD). In temperate grasses there are around 20 *CBF* genes which are likely to have partly differentiated roles.

3. Can We Increase Spring Productivity at High Latitudes?

Unlike the situation in autumn, it is not light availability, but temperature, which is currently limiting biomass production in spring at high latitudes (Figure 1). Thus, there is a potential to utilize an earlier thermal growing season in the future. However, with the growing season starting earlier in the year, and possibly before the spring equinox, the day-night temperature amplitude and the probability of night frost or longer freezing periods increases. For example, the probability of spring frost damage was predicted to increase in the western part of the Nordic area in 2040–2065 as compared to 1960–1990 [5].

In general, exposure to higher temperatures in spring results in stimulation of growth and at the same time, loss of freezing resistance (de-acclimation) [20]. There are several reports describing de-acclimation and re-acclimation responses in perennial grass species [99–105], and some of them also report a negative association between freezing resistance and leaf growth during the de-acclimation period. In cereals, it has been shown that both freezing resistance and expression of cold-induced genes are down-regulated in shoot base tissue when the vernalization requirement is saturated, but before any development of the apex is visible in the microscope [106–108]. There is an interaction between vernalization and photoperiod on de-acclimation. In cultivars with a long day requirement for flowering, the negative effect of vernalization on freezing resistance is stronger when plants are vernalized under long days than under short days, whereas vernalization- and photoperiod-insensitive cultivars are not able to develop much freezing resistance at all [109–112]. Also, plants vernalized and de-acclimated under long days are often found to be less able to re-acclimate [113,114]. Vernalization not only enhances de-acclimation, as well as competency to flower in response to long photoperiod in a large number of perennial grass species [19], but also increases the rate of leaf expansion, specific leaf area, and photosynthetic rate of perennial ryegrass leaves developed after transfer to 15 °C, particularly under long photoperiods [115].

In order to utilize more of the spring light for increased productivity, it would be necessary to grow plants that are capable of maintaining freezing tolerance during early spring growth, and/or able to rapidly re-acclimate upon demand. In this context, it would be desirable to have a better understanding of (1) how do temperature, vernalization, and photoperiod together control leaf growth and freezing resistance in spring? and (2) which mechanisms govern rapid re-acclimation after de-acclimation, and to which extent do these function in growing plants?

3.1. Regulation of Leaf Growth versus Freezing Resistance in Spring

VRN1, an inducer of the transition to generative development in cereals and other temperate grass species, is gradually up-regulated during vernalization [116,117]. Several studies indicate that there is a negative association between expression level of *VRN1* and the expression of cold-induced genes and freezing resistance. Using near-isogenic lines of wheat and barley, and a *T. monococcum* deletion mutant, it was shown that, under 16 h photoperiod, the *VRN1* locus controls expression of *VRN1*, *COR14B*, and other cold induced-genes [106–108,112,118]. High expression levels of *VRN1* were associated with the down-regulation of cold-induced genes and freezing resistance. From these studies, however, it is not entirely clear whether it is *VRN1* itself, or very closely linked genes, that is responsible. However, using a transgenic approach combined with chromatin immunoprecipitation sequencing and RNA sequencing, Deng et al. [119] showed that in barley grown at 16 h photoperiod, *VRN1* binds to the promoter of several *CBF* genes. After short-term cold exposure, when the expression level of *VRN1* is still very low, Oliver et al. [120] found similar kinetics in the initial transcription of *VRN1* and *COR14B* upon cold exposure (24 h) in barley. Under short photoperiods, high *COR14B* expression or positive correlation between expression of *VRN1* and *COR14B* remained after long-term cold treatment in *T. monococcum* [112], barley [121], and meadow fescue [105]. *COR14B* is induced by *CBFs*, and barley *VRN1* also has a putative *CBF* binding site in its promoter [122]. Oliver et al. [107] therefore suggested that *VRN1* and *COR14B* may be regulated by similar mechanisms in early cold acclimation, possibly through the action of *CBF* transcription factors. Several studies show that *CBF6* and *COR14B* are down-regulated in cereals and meadow fescue by prolonged cold, but only under long photoperiods [105]. Taken together, these results suggest that *VRN1* and the *CBF* regulon are co-regulated during cold acclimation of temperate grasses and as long as photoperiods are short, but that *VRN1* down-regulates *CBFs* when photoperiods become long (Figure 3). This is a possible explanation for the interaction between vernalization and photoperiod during de-acclimation in temperate grasses. Also, given that *CBFs* can inhibit leaf growth via GA and DELLA proteins [34], the regulatory effect of *VRN1* on *CBF* expression may explain the effects of vernalization on leaf growth and photosynthetic activity observed by Stapleton and Jones [115], and also its interaction with photoperiod.

3.2. Is Re-Acclimation in Spring Different from Cold Acclimation in Autumn?

Under controlled conditions, the re-acclimation of temperate grasses differs somewhat from the initial cold acclimation. For example, carbohydrates did not accumulate to the same extent during re-acclimation as during initial cold acclimation in winter wheat [114], and several cold induced genes upregulated by cold acclimation in meadow fescue were not upregulated during re-acclimation [105]. The mechanisms behind these differences are not known, but are likely to be related to a coordinated regulation of growth and freezing tolerance as described in Section 2.3. In the field, re-acclimation may also be inhibited if plants are exhausted from carbohydrate reserves or devoid of functional leaf area. Re-acclimation at a time when spring growth has been initiated may be provided by other mechanisms than those employed during initial cold acclimation in the autumn. For example, while expression of *COR14B* could explain some of the variation in freezing resistance in de-acclimated meadow fescue, *CR7* was, unlike *COR14B*, significantly upregulated by re-acclimation and could explain some of the variation in freezing resistance after re-acclimation [105].

4. Conclusions

The expected prolonged growing season in future autumns can probably be utilized for higher autumn productivity in some areas, but in areas where photosynthesis is prohibited during long winters, such as at high latitudes, areas with a deep long-lasting snow cover, or with severe stresses killing leaf blades, this may not be possible due to the need for storage carbohydrates. There is a larger potential for utilizing the earlier springs to increase productivity in such areas, but it will be necessary with

varieties that maintain some level of freezing resistance and re-acclimation ability also during early spring regrowth.

The many *CBF* genes in perennial grasses, which are differentially regulated and probably have different functions, could possibly be utilized in developing varieties that combine some autumn productivity with cold acclimation. Similarly, a possibility of at least partly breaking the association between growth, de-acclimation, and loss of re-acclimation ability in spring may lay in playing with alleles of the various *CBF* genes and their differential functions. The interaction between temperature and light factors, particularly photoperiod, on *CBF* regulation is critical in this respect. An improved understanding of the specific functions of the various *CBF* genes—how they are regulated and which parts of the *CBF* regulon they control, as well as an overview of allelic variation—could aid in the development of perennial grass varieties with an optimal balance between growth and perennial persistence under future climates.

Conflicts of Interest: The author declares no conflict of interest.

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