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Review

How can forage production in Nordic and Mediterranean Europe adapt to the challenges and opportunities arising from climate change?

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ABSTRACT

Climate change and its effects on grassland productivity vary across Europe. The Mediterranean and Nordic regions represent the opposite ends of a gradient of changes in temperature and precipitation patterns, with increasingly warmer and wetter winters in the north and increasingly warmer and drier summers in the south. Warming and elevated concentration of atmospheric CO_2 may boost forage production in the Nordic region. Production in many Mediterranean areas is likely to become even more challenged by drought in the future, but elevated CO_2 can to some extent alleviate drought limitation on photosynthesis and growth. In both regions, climate change will affect forage quality and lead to modifications of the annual productivity cycles, with an extended growing season in the Nordic region and a shift towards winter in the Mediterranean region. This will require adaptations in defoliation and fertilization strategies. The identity of species and mixtures with optimal performance is likely to shift somewhat in response to altered climate and management systems. It is argued that breeding of grassland species should aim to (i) improve plant strategies to cope with relevant abiotic stresses and (ii) optimize growth and phenology to new seasonal variation, and that plant diversity at all levels is a good adaptation strategy.

1. Climate change and Nordic versus Mediterranean grasslands

The most contrasting regions of Europe in terms of climate are the Mediterranean and the Nordic regions, representing a latitudinal gradient in temperature (Metzger et al., 2005). Within these regions, there are gradients in both oceanicity and precipitation. According to the environmental classification and stratification of Europe made by Metzger et al. (2005), the largest environmental zones in the Nordic region are the Alpine North and the Boreal zones, but in the southern part of this region there are also Nemoral, Atlantic North and Continental zones. There is a strong west to east gradient of decreasing precipitation in the Nordic region. The Mediterranean region of Europe has a complex pattern of environmental zones (Mediterranean South, Mediterranean North and Mediterranean Mountains), largely determined by temperature (Metzger et al., 2005). While forage production from grasslands are limited by cold and dark winters in the Nordic region, it is limited by hot and dry summers in the Mediterranean region. Across Europe, climate change could raise significant challenges for grassland-based food production and other ecosystem services provided by grasslands, but may also imply some opportunities. The observed and projected climate change differs between Northern and Southern Europe (Kovats et al., 2014, Table 1). The average temperature over land surface during 2002–2011 was 1.3 °C above the 1850–1899 average, with substantial differences between regions and seasons. In the Nordic region, both the observed and predicted warming is more rapid than the global average warming. Annual average temperatures have increased with more than 2 °C during 1847–2013, almost twice the global average increase, and both the observed and the predicted temperature increase is highest during late autumn, winter and spring (Uleberg et al., 2014; Mikkonen et al., 2015;

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Table 1
The main climatic changes and their effects in Nordic vs. Mediterranean grasslands during the growing season and the unfavorable season.

Growing season	Current timing	Nordic April–early June to Mid-September–early November[1]	Mediterranean October–June
	Predicted seasonal changes	1) Extension of thermal growing season by 1–3 months by the end of the century[2,3] 2) Increase in temperature and precipitation[a,3–7]	1) Growing season will shift towards winter[17,18] due to drier summers and warmer winters 2) Higher temperatures and more frequent droughts[4,20–22]
	Effects on productivity	1) Increase in productivity if plant available water does not become limiting[1] 2) Lengthening of growing season can be utilized mostly in spring due to lack of light in late autumn[8,9] 3) One extra cut per year in many regions[1]	1) Increase in productivity when water is not limiting, higher CO_2 concentration will limit yield reduction due to drought stress[17,18,23]
	Plant material and breeding needs	1) More intra- and interspecific diversity, broader genetic material with more response diversity[10,11] 2) Higher regrowth capacity 3) Maintenance of growth in water-saturated soils and during dry spells	1) More intra- and interspecific diversity[24–26] 2) Utilization of cooler parts of the year for increased growth 3) Maintenance of growth under moderate drought

Unfavorable season	Current timing	Nordic Mid-September–early November to April–early June[1]	Mediterranean June–early October
	Predicted seasonal changes	1) Shorter winters with more precipitation and higher temperatures[4,5,7,12] 2) Delayed cold acclimation/growth cessation and earlier deacclimation/spring regrowth[9] 3) Decrease or increase in snow cover, soil frost and ice encasement, depending on temperature level, precipitation and interactions between them[13–16]	1) Longer summers with higher temperatures and more frequent and severe droughts and heat waves[4,20,21] 2) Altered timing or conditions during critical phases of life and growth cycles[27–29]
	Effects on productivity	1) Increased or decreased winter mortality due to higher or lower stress levels and changes in growth cycle, plant C and N acquisition and use, acclimation and deacclimation[1,9,17]	1) Decreased productivity or longer non-productive dry season, higher summer mortality[17,18]
	Plant material and breeding needs	1) More intra- and interspecific diversity, broader genetic material with more response diversity[10,11] 2) Utilize earlier spring and later autumn without losing ability to survive winters[9]	1) More intra- and interspecific diversity[24–26] 2) Stronger summer dormancy and active recovery after drought in perennials[30–32] 3) more persistent seed banks of annuals[33–35]

References: Höglind et al. (2013)[1], Ruosteenoja et al. (2011)[2], Hanssen-Bauer et al. (2015)[3], Lehtonen et al. (2014)[4], Uleberg et al. (2014)[5], Mikkonen et al. (2015)[6], Ruosteenoja et al. (2016)[7], Ruosteenoja and Räisänen (2013)[8], Ergon (2017)[9], Mäkinen et al. (2015)[10], Mäkinen et al. (2016)[11], Ruosteenoja et al. (2007)[12], Källomäki et al. (2010)[13], Räisänen and Eklund (2011)[14], Johansson et al. (2011)[15], Bjerke et al. (2015)[16], Rapacz et al. (2014)[17], Graux et al. (2013)[18], Dono et al. (2016)[19], Giorgi and Lionello (2008)[20], Giannakopoulos et al. (2009)[21], Hoerling et al. (2012)[22], Roy et al. (2016)[23], Porqueddu and Maltoni (2014)[24], Maltoni et al. (2007)[25], Barkaoui et al. (2016)[26], Ooi (2012)[27], Cosentino et al. (2014)[28], Long et al. (2015)[29], Volaire et al. (2014)[30], Norton et al. (2016)[31], Kallida et al. (2016)[32], Sulas (2005)[33], Salis et al. (2012)[34], Porqueddu et al. (2016)[35].

[a] change associated with high uncertainty.

Ruosteenoja et al., 2016). The length of the thermal growing season has increased with about 1–2 weeks during the last 30 years, and has been predicted to become 1–3 months longer by the end of the century as compared to the period 1971–2000 (Ruosteenoja et al., 2011; Hanssen-Bauer et al., 2015). Annual precipitation in the Nordic region is predicted to increase considerably (up to around 20% relative to 1971–2000 in some regions) by the end of the century, with more frequent episodes of extreme precipitation, and especially during winter (Lehtonen et al., 2014; Hanssen-Bauer et al., 2015). In the Mediterranean region, the climate is expected to become warmer and drier, particularly in summer (Giorgi and Lionello, 2008; Giannakopoulos et al., 2009; Lehtonen et al., 2014). Winters are also expected to become warmer, but to a lesser extent than summers, while winter precipitation may vary between regions (Giorgi and Lionello, 2008; Giannakopoulos et al., 2009; Hoerling et al., 2012). Increased inter-annual variability in summer and winter precipitation, as well as in summer temperatures, is also expected (Giorgi and Lionello, 2008). Changes in atmospheric CO_2 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 the individual leaves to agroecosystems (Hatfield and Prueger, 2011; Xu et al., 2013). For grasslands, there are also important complicating factors such as plant competition and other plant–plant interactions, perennial growth habits, seasonal productivity patterns, and plant-animal interactions (Porter et al., 2014).

Grasslands comprise a variety of vegetation types and management systems (e.g. Allen et al., 2011; Huyghe et al., 2014; Peeters et al., 2014). A distinction is made between temporary and permanent grasslands. Temporary grasslands, also termed forage crops, are regularly re-established (annually or at longer intervals), or constitute an element in a crop rotation. Permanent grasslands are grasslands that have either never been ploughed or not been ploughed for at least five to ten years (definitions vary). Permanent grasslands can range from natural and semi-natural (not managed by other means than grazing or mowing) to agriculturally improved permanent grasslands (i.e. improved by fertilization). Both temporary and permanent grasslands may be harvested by mowing (meadows), grazing (pastures) or a combination, and consist of perennial, biennial and/or annual forage species, mainly grasses and legumes. Overviews of grassland production in the Nordic and Mediterranean regions of Europe were recently given by Helgadóttir et al. (2014) and Porqueddu et al. (2016). Nordic grasslands are dominated by perennial grasses, with a few perennial legume species also present. Annual species are used only to a limited extent. There are both permanent and temporary grasslands, which are grazed or mown. Due to the lack of plant growth during winter, there is a strong reliance on harvested and conserved forage. In Mediterranean Europe, grasslands can be grazed from autumn to spring and may be mown in spring for hay production. Permanent grasslands can be dominated both by perennial and annual grasses, while temporary grasslands are often dominated by annual species. In summer, forage production can be completely or very limited by drought. Agro-silvo-pastoral systems are important in some areas. Annual and perennial grasses and legumes such as alfalfa (*Medicago sativa* L.) are to some extent cultivated as forage crops, which are sometimes irrigated. We

here review the current research available related to the challenges and opportunities for forage production associated with changing climate in these two contrasting regions. We consider challenges and opportunities created by climate change in terms of forage productivity, forage quality and plant species composition (Section 2), while also assessing how utilization of plant traits and management practices could enable adaptation (Section 3). Although intimately linked to forage production, livestock production and the integration of mitigation and adaptation strategies is not within the scope of the present paper.

2. What are the challenges and opportunities of climate change in Nordic versus Mediterranean grasslands?

2.1. Forage dry matter productivity

In the Nordic region, the short growing season generally limits agricultural production (Peltonen-Sainio et al., 2009). Thus, longer growing season is favourable, especially in spring when water supply and solar radiation is optimal for growth. In a modelling study, Höglind et al. (2013) found 11% increase in annual dry matter (DM) yields of timothy (*Phleum pratense* L.) in northern Europe in 2040–2065 as compared to 1960–1990, with the largest increases in the western regions which were less water-limited than the eastern regions. This study assumed that farmers adjusted the timing and number of harvests, and that nutrient conditions were optimal, but did not take the effect of elevated CO_2 on growth into account. Elevated atmospheric CO_2 concentration has the potential to increase photosynthetic rates and biomass production of C_3 plants (Ainsworth and Long, 2005; Soussana and Lüscher, 2007). In a study of timothy and lucerne mixtures in eastern Canada, which did take the effect of elevated CO_2 into account, 5–35% increase in DM yield in 2020–2079 relative to 1971–2000 was estimated (Thivierge et al., 2016). This occurred despite an increase in the duration of periods when high temperatures or water shortages limited the productivity. However, there are large uncertainties in the predictions. In pure grass stands the positive effect of temperature and CO_2 on yield may be limited by N (Leakey et al., 2009; Piva et al., 2013), and it may not be possible to utilize all of the extended thermal growing season. Although temperatures increase, the unique photoperiod in Northern latitudes remains unchanged. Short days and low inclination of incoming solar radiation in autumn can limit the amount of photosynthetically active radiation to the point that it becomes a restricting factor for growth, particularly at higher latitudes (Ruosteenoja and Räisänen, 2013; Uleberg et al., 2014; Virkajärvi et al., 2015).

There are many uncertainties regarding winter stresses in a future climate (Rapacz et al., 2014). The type and severity of winter stresses depends not only on the minimum temperature during winter, but also largely on the presence or absence of a snow cover, and on factors that control the cold acclimation status of the plants. Decrease in long-term mean snowpack has been predicted toward the end of the century, although individual snow-rich winters will still occur (Räisänen and Eklund, 2011). Thus, there will be shorter duration of snow cover and eventually snow-free winters in some regions now characterized by stable snow cover. On the other hand, increased precipitation in areas where temperatures remain below freezing can give longer-lasting snow cover in some areas (Johansson et al., 2011). Less snow cover can increase the occurrence, depth and duration of soil frost due to less insulation (Källomäki et al., 2010; Bjerke et al., 2015), and was shown to affect annual productivity of grasslands in Canada and Germany (Vankoughnett et al., 2016; Zeeman et al., 2017). There has been an increase in frequency of winter warming events in northern Norway, Sweden, and Finland during the last 50 years (Vikhamar-Schuler et al., 2016). This has led to increased numbers of melt-days during winter by 3–7 days per decade, and a further increase in such events are projected. The combination of increased precipitation in the autumn and winter, milder and unstable temperatures, and frozen soils, may lead to ice cover or waterlogging. The risk of winter damage is expected to increase east of the Baltic Sea, even for the winter hardy species timothy, while the risk of spring frost damage is predicted to increase in the western part of the Nordic area (Höglind et al., 2013). In winter, when solar irradiation is insufficient for photosynthesis in northern latitudes, the carbon-economy and survival of the plants becomes increasingly important when temperatures exceed 5 °C and respiration increases. On the other hand, if temperatures remain cool, shorter winters could leave more C and N reserves in spring, increasing survival and spring DM production (Jing et al., 2013; Piva et al., 2013). Higher temperatures in autumn will shift cold acclimation of the plants to a time when less light is available. This can have impacts on growth cessation and cold acclimation of plants (Østrem et al., 2014; Dalmannsdottir et al., 2017; Ergon, 2017), rendering them more vulnerable to winter stresses. In addition, waterlogged soils in combination with higher autumn temperatures have negative effects on cold acclimation of timothy (Jørgensen et al., 2016). Unstable winter temperatures and early springs can cause plants to de-acclimate, when there is still a risk of freezing (Jørgensen et al., 2010; Rapacz et al., 2014). The distribution of many weeds, pests and pathogens are limited to the north by harsh winters. With global warming, many of these species can be expected to spread northward (Jepsen et al., 2011; Juroszek and von Tiedemann, 2013; Svobodová et al., 2014).

More severe and frequent droughts leading to reduced productivity through both reduced growth and reduced persistence, is considered the major climate challenge for forage production in the Mediterranean region in the future. The direct effect of heat stress is not likely to be of the same importance in grasslands as in grain crops, where heat stress during certain stages of reproductive development can be detrimental for yields. In the Mediterranean region, water availability will often be more limiting for photosynthesis than the atmospheric CO_2 concentration, but CO_2 concentration still has important effects due to interactions with temperature and drought. Elevated CO_2 can partly compensate for the reduced CO_2 influx through stomata under moderate drought (Ainsworth and Long, 2005; Soussana et al., 2010). Consequently, elevated CO_2 enhances biomass production and improves water relations under drought (Clark et al., 1999). In addition, elevated CO_2 contributes to water sparing (reduced transpiration due to less stomatal opening) during periods when sufficient water is available, leaving more water for later in the season, when the water reserves might otherwise be exhausted (Morgan et al., 2004).

In Mediterranean Europe, the productivity of rainfed grasslands is limited during the dry summer. Changes in the seasonal patterns of temperature and precipitation are likely to shift productivity further towards cooler and wetter parts of the year. Projections of climate change impact on grassland productivity (Graux et al., 2013) indicated that summer yields may be reduced in Mediterranean France in the far future (2070–2099). However, in this study higher yields were predicted in autumn, winter and spring due to a combined effect of higher temperatures and CO_2 levels, leading to an overall increase in productivity. In line with this, Dono et al. (2016), modelling productivity of semi-natural grasslands dominated by self-reseeding annual species (no summer production) in the near future (2020–2030) in Sardinia, Italy, predicted decreased spring yields and higher autumn yields due to increased temperature and increased rainfall occurrence in October. In the same study, irrigated annual ryegrass crops were predicted to have increased yields in the near future. Model-based studies are affected by uncertainties and assumptions and, as Graux et al. (2013) pointed out, their study neither accounted for a possible increase in mortality of perennials during summer droughts, nor climate change-induced changes in species composition, both factors that may have importance in grasslands.

In summary, grassland productivity can be expected to increase in the Nordic region, and shift towards winter in the Mediterranean region, except on relatively moist or irrigated land (Table 1, Fig. 1).

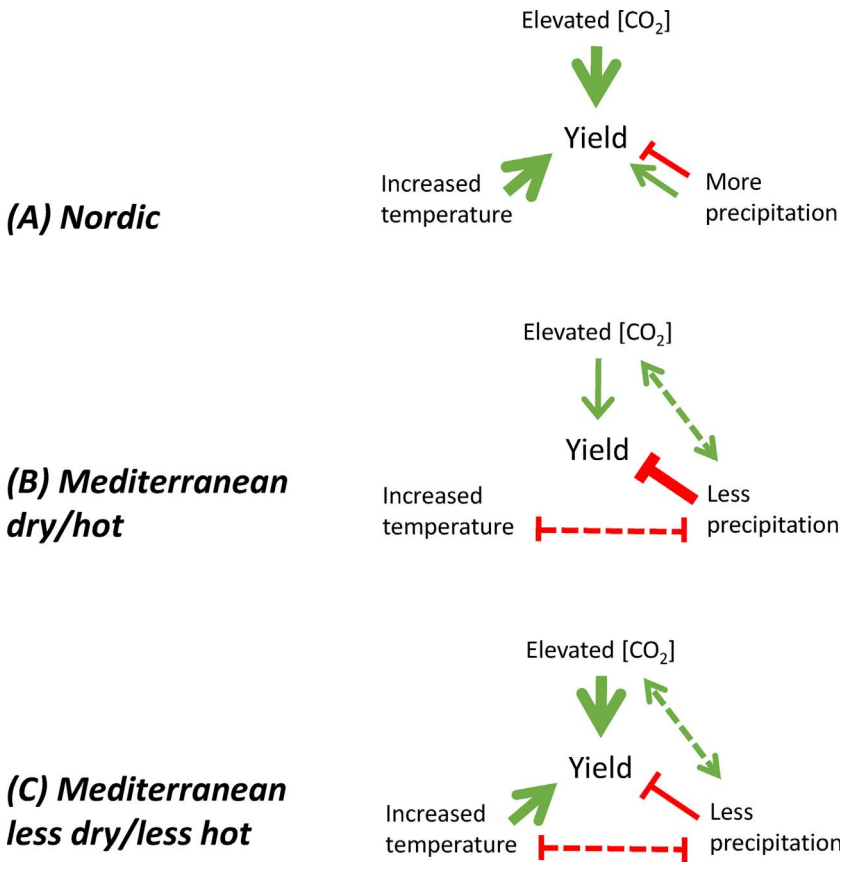


Fig. 1. Effects of climate change on forage production. Temperature, atmospheric [CO_2] and precipitation can all affect grassland yields (positive effects indicated by pointed arrows and negative effects indicated by blunted arrows). In addition, they interact (indicated by broken lines): elevated [CO_2] improves drought tolerance under moderate drought due to a decrease in stomatal conductance, and higher temperatures promotes drought by increasing evapotranspiration, while drought reduces evaporative cooling and exacerbates heat stress. (A) In the Nordic region increased temperature and elevated [CO_2] will increase grassland productivity during the growing season. More precipitation will probably have a positive effect on productivity in many areas, but can also have negative effects through water logging, soil compaction and nutrient leakage. In the Mediterranean region, the negative effect of less precipitation will override the positive effect of elevated [CO_2] during summer and in dry regions (B), but during the rest of the year, and in less dry areas, the positive effects of increased temperature and elevated [CO_2] will override the negative effect of less precipitation (C).

2.2. Forage quality and species composition

Climate change may affect forage quality in different ways. Higher temperatures lead to earlier stem elongation, a faster rate of decline in cell wall digestibility of both vegetative and reproductive tillers during aging, and hence faster decline in the digestibility of forages (Groot et al., 2003; Thorvaldsson et al., 2007; Bertrand et al., 2008; Bloor et al., 2010; Jing et al., 2013). In addition, higher standing biomass is associated with higher stem-to-leaf proportions and lower digestibility, at least in timothy (Bélanger and McQueen 1998; Bélanger et al., 2001), and thus climate change may lead to lower or higher digestibility through its effect on growth rate, stand density and competition for light. The effects of phenological development and standing biomass can largely be compensated by changes in defoliation regimes and fertilization (discussed below). Climate change may also affect forage quality through effects on species composition. Elevated CO_2 tends to increase the competitive ability of legumes in legume-grass mixtures, if the legumes are not limited by minerals such as phosphorous (reviewed by Lüscher et al., 2004; Soussana and Lüscher, 2007; Soussana et al., 2010). This may compensate for the slight decrease in protein content of grasses at elevated CO_2 (Soussana and Lüscher, 2007; Dumont et al., 2015). Dumont et al. (2015), in their meta-study of climate change effects on forage quality, found that elevated CO_2 did not affect digestibility, but increased the total non-structural carbohydrate content by an average of 25% and decreased N content by 8%, reflecting the shift in the C:N-ratio of the environment. N content increased with increasing drought level, and unlike other sites, a decrease in herbage N concentration in response to elevated CO_2 was not found at Mediterranean sites. The authors suggested that this could be due both to water limitation on growth, and changes in species composition (higher legume proportion), leading to higher concentration of N in the forage. In some Mediterranean regions, e.g. in semi-arid Italy, semi-natural grasslands are dominated by annual species that are maintained by seed banks (Cosentino et al., 2014). The species composition in these grasslands varies between years, depending on previous seed production, dormancy and germination. These are all processes strongly influenced by climatic conditions such as temperature and moisture, and therefore most likely affected by climate change (Ooi, 2012; Cosentino et al., 2014; Long et al., 2015).

3. How to address these challenges and opportunities?

Grassland management targets an optimal balance between forage yield, forage quality, yield stability and persistence (plant survival or reproduction). This can be achieved through a suitable choice of plant material, optimization of the defoliation and fertilization strategies, irrigation, drainage, soil management, control of unwanted organisms, and renovation or re-establishment of the grassland.

3.1. Choice of plant material

Choosing the best species and mixtures for sown grasslands can be a way to meet challenges and utilize opportunities raised by climate change. A harsh winter climate is the strongest limiting factor determining which perennial species can be cultivated in the Nordic region. Although there is considerable uncertainty regarding winter survival in the future, a longer growing season and milder winters may increase the prospective for using species and cultivars with higher yield potential and feeding value. Currently, winter hardy species such as timothy, meadow fescue (*Schedonorus pratensis* Huds. syn. *Festuca pratensis* Huds.) and red clover (*Trifolium pratense* L.), are widely used (Helgadóttir et al., 2014). Species like perennial ryegrass (*Lolium perenne* L.) and festulolium (×*Festulolium* Aschers. et Graebn.) are used in the southern Nordic area, and are of increased interest for the future climate also further north because of their high production capacity throughout the growing season as well as high nutritive value (Østrem

et al., 2013). Including deep-rooted drought tolerant species like tall fescue (*S. arundinaceus* Schreb. *syn. F. arundinacea* Schreb.), fescue type festulolium, cocksfoot (*Dactylis glomerata* L.), red clover and lucerne in the mixtures can be a strategy to prevent yield reduction during drought periods. Tall fescue has a better nitrogen uptake, nitrogen use efficiency and water use efficiency, and a yield potential which is up to 50% higher than perennial ryegrass in dry periods, most probably owing to its deeper rooting system (Cougnon, 2013; Cougnon et al., 2017). In addition, it can tolerate poorly drained soils (Barnes et al., 2003). However, the digestibility and animal preference is lower than in perennial ryegrass (Cougnon et al., 2014). Cultivation of whole crop maize (*Zea mays* L.) has increased during the last decades and the expected climate changes will further promote this development, at least in southern parts of the Nordic region (Elsgaard et al., 2012). This could be compatible with an increased use of legumes and total mixed ratio feeding strategies, where high protein forages can be complemented with low protein but high energy components, and thereby influencing what type of grasslands will be cultivated.

A wide range of annual forage species showing adaptability to Mediterranean climate conditions are currently available in the market (e.g. oat (*Avena sativa* L.), italian ryegrass (*L. multiflorum* Lam.), crimson clover (*T. incarnatum* L.), egyptian clover (*T. alexandrinum* L.), common vetch (*Vicia sativa* L.)) (Annicchiarico et al., 2013; Porqueddu et al., 2016). Despite an increasing use of annual self-reseeding species (mainly subterranean clover (*T. subterraneaum* L.) and *Medicago* spp.) for pasture improvement in dry environments (Porqueddu and Gonzalez, 2006), cultivars available in the seed market have often proved to be poorly adapted to the climatic conditions and management systems of Mediterranean Europe (Sulas, 2005; Salis et al., 2012; Porqueddu et al., 2016). Native genotypes of these species (e.g., rigid ryegrass (*L. rigidum* Gaud.) and burr medic (*M. polymorpha* L.)) have been selected (Porqueddu, 2001; Franca et al., 2005), but not adopted by the seed industry in Europe so far. Perennial forages such as tall fescue or cocksfoot can be a valuable alternative to annuals, if they can survive across successive summer droughts. Although most of the temperate origin cultivars available on the market are not drought persistent in Mediterranean areas (Lelièvre and Volaire, 2009), a few cultivars with summer dormancy (Volaire and Norton, 2006) can tolerate severe successive droughts and survive in environments with annual rainfall as low as 300 mm (Annicchiarico et al., 2011; Pecetti et al., 2009, 2011). Under chronic water shortages, perennial forage species have a number of advantages in comparison to the predominantly used annual species including (i) fewer inputs with less field preparation and fertilizer requirement, (ii) year-around soil cover reducing the risk of intense soil erosion, (iii) optimal use of water throughout all seasons, thus enhancing forage production in particular in autumn when cereals and annual species are not yet established and (iv) greater flexibility because of the multiple uses of these species (grazing, hay, silage). Therefore, perennial species are an excellent alternative to annual species, contributing to reduced production costs, to halt rangeland degradation and overall to confer greater security to rain-fed agricultural systems (Lelièvre and Volaire, 2009; Volaire et al., 2016). Cultivars of bulbous canary-grass (*Phalaris aquatica* L.) and tall fescue that express summer dormancy play an increasing role in eastern Australia and the semi-arid environment of the Southern Great Plains in the USA, and can be used in regions with down to about 550–500 mm precipitation per year (Oram and Lodge, 2003; Malinowski et al., 2005, 2009; Norton et al., 2016). Such cool season grasses were also found to be quite productive and successful in south-west Australia (Rogers et al., 1976; Biddiscombe et al., 1977) although until recently they have been poorly adopted by the seed industry. The association of summer dormant grasses and Mediterranean type alfalfa, combining the dehydration tolerance of the grass and the dehydration avoidance of the legume provides high functional complementarity for water use in summer and is advocated for drought prone areas (Volaire et al., 2016).

Unstable conditions with large variation in weather within and between seasons increase uncertainty in forage production. Diversity among responses to critical weather factors improves resilience at both sward and farm level (Mäkinen et al., 2015). Seed and variety mixtures with components that have both desired traits and complementary niches can exploit temporal and spatial variation in environmental conditions, and be more stable and robust compared to monocultures or simple mixtures. Using mixtures is therefore considered a key strategy to maintain production in unpredictable and unstable environments (Maltoni et al., 2007; Volaire et al., 2014; Lüscher et al., 2014). Species and variety mixtures also tend to be more stable in forage quality than pure stands of one species (Sleugh et al., 2000; Sanderson, 2010; Ergon et al., 2017), and therefore allows for some flexibility in harvest times, which is desirable in rainy summers in the Nordic region. It may be possible to design optimized mixture compositions based on detailed experiments (Goslee et al., 2013). For example, mixtures of summer-dormant and summer-active perennial species may provide stable pastures exploiting available soil moisture throughout the year in some Mediterranean regions (Norton et al., 2016). Similarly, grass-legume mixtures including both annuals and perennials proved to achieve higher yields and utilize a longer period for growth than pure stands, under dry Mediterranean conditions (Porqueddu and Maltoni, 2007; Maltoni et al., 2007). However, when a single environmental factor is dominant, yield and survival may depend largely on a specific trait rather than on functional diversity. For example, under severe summer water deficit, rooting depth enhanced water uptake and resilience of grass communities irrespectively of the level of species diversity in the communities (Barkaoui et al., 2016). Including N-fixing legumes in mixtures has several advantages, and can facilitate a better exploitation of elevated atmospheric CO_2 concentration (Lüscher et al., 2004, 2014). However, since legumes require relatively high amounts of K and P, nodulation and N fixation may become limited by low nutrient supply and high or low temperatures (Nesheim and Boller, 1991; Irigoyen et al., 2014), and the conservation of legume forage can be challenging, particularly in a wet Nordic climate.

3.2. Breeding for the future climate

In order to meet the challenges and utilize the opportunities that climate change will bring, the plant material we cultivate should (i) exhibit growth cycles that better fit the new seasonal climate patterns, (ii) be able to cope with relevant stresses and have the right balance between growth potential, nutritive value and stress tolerance, and (iii) have the phenotypic plasticity or genetic diversity within populations that ensures yield stability under variable and unpredictable conditions.

The annual recurrent periods of winter stresses or summer droughts have led to the evolution of seasonal acclimation and de-acclimation processes regulating the level of resistance to seasonal stresses in perennial grasses (Laude, 1953; Volaire and Norton, 2006; Preston and Sandve, 2013). These processes, which are largely regulated by temperature and photoperiod, correlate with changes in growth, reproductive development and dormancy status (Preston and Sandve, 2013; Norton et al., 2009; Gillespie and Volaire, 2017), and latitudinal clines in responses to temperature and photoperiod have been described (Cooper, 1964). With global warming, there will be new combinations of temperature and photoperiod. This is particularly the case in the north where photoperiod changes dramatically during the course of a year. In order to utilize a longer growing season in Nordic Europe, and a shift in the growing season in Mediterranean Europe, we need species and varieties with temperature and photoperiod responses conferring an annual growth pattern that optimizes growth during the favourable part of the year and survival during the cold Nordic winter or dry Mediterranean summer (Ergon, 2017). Resistance to winter stresses are still likely to be of high importance in the Nordic region in the future (see Section 1). Plants encounter many stresses during winter: freezing, anoxia due to ice encasement or water-saturated soils, soil movements due to freeze-thaw cycles, winter pathogens, starvation

and dehydration due to frozen soils. Specific resistance mechanisms to these stresses exist, but they are also largely interconnected through genetics and physiology. Central to winter survival is proper cold acclimation in autumn and sufficient maintenance of a cold acclimated state in spring. During cold acclimation, leaf elongation ceases, a number of stress responses are elicited, and organic reserves accumulate. Both cold acclimation in autumn and deacclimation in spring are mainly controlled by temperature. However, light is also important in at least three different ways: (i) high irradiance combined with low temperature increases the photosystem II excitation pressure, eliciting signalling pathways leading to cold acclimation, (ii) light is the energy source for the accumulation of organic reserves, and (iii) photoperiod is a developmental signal influencing growth, cold acclimation and deacclimation. Due to these reasons, the shift of cold acclimation and deacclimation into shorter photoperiods may affect the ability of plants to cope with winter stresses (Dalmannsdottir et al., 2017). A more detailed and quantitative understanding of interactions between temperature and light on winter survival in different species is needed. Breeding activities may need to focus on adjusting the timing of growth cessation and cold acclimation in autumn, and the opposite process in spring, to new temperature and photoperiod combinations. For example, at high latitudes, perennial ryegrass and festulolium tend to cease growth in autumn too late for sufficient cold acclimation (Østrem et al., 2014). It will however, be necessary to manage the trade-off between optimal timing with respect to winter survival, and utilization of the longer growing season to increase production (Ergon, 2017). In order to utilize the potential for higher productivity in the north, there is also a need for strong regrowth capacity and tolerance to more frequent harvesting or grazing. For timothy, the priorities would likely be to improve tolerance to harvesting and grazing, better regrowth capacity and spring growth. Perennial ryegrass needs better winter survival, particularly improved timing of growth cessation and cold acclimation, as well as resistance to psycrophilic pathogenic fungi (Abdelhalim et al., 2016), while for tall fescue, work is ongoing to combine the high yield and drought tolerance with an acceptable digestibility and animal preference (Humphreys et al., 2012; Helgadóttir et al., 2014; Cougnon et al., 2015; Fariaszewska et al., 2016).

Drought escape (i.e. when plants survive the dry summer as seeds; Long et al., 2015) and hardseededness (which allows a more persistent seed bank; Taylor, 2005) are the main adaptive strategies of annual species in Mediterranean grasslands. Based on the predicted changes in precipitation, with an overall reduced growth period in the driest Mediterranean regions, annual species will need earlier seed maturation for reliable seed set in shorter growing seasons, as well as mechanisms (i.e. regulation of seed dormancy and germination) ensuring the presence of a seedbank under the expected seasonal patterns of temperature and water availability (Porqueddu et al., 2016). A low requirement for dormancy release gives the potential for early germination and higher yield, but at the risk of seedling mortality due to false breaks. Given the uncertainty and the expected climatic variability, intra- and interspecific variation in regulation of dormancy release in cultivars and seed mixtures appears to be a good strategy. In the past, breeding efforts in tall fescue and cocksfoot have mainly been directed towards use in temperate areas with summer active material that are short lived under drought, and there are therefore very few cultivars adapted to severe drought currently available in southern Europe (Lelièvre and Volaire, 2009). Persistence during severe drought is governed by mechanisms different from those conferring resistance to moderate droughts (Milbau et al., 2005; Volaire et al., 2009). Plants with responses resulting in resistance under moderate drought and maintenance of shoot growth have to either avoid or tolerate leaf dehydration. At moderate drought, the maintenance of biomass production can be achieved primarily by maximizing soil water capture while maintaining stomatal gas exchange and transpiration (Blum, 2009). A deep root system with a high density of roots at depth (Carrow, 1996; Wasson et al., 2012; White and Snow, 2012) and maintenance of leaf area, leaf relative water content, leaf cell turgor and photosynthetic capacity (Morgan, 1988; Serraj and Sinclair, 2002) are traits that are associated with high yield in water-limited environments. Plant responses resulting in survival under severe drought, however, are mainly associated with growth cessation, dehydration avoidance and tolerance occurring in young tissues including basal meristematic tissues. When conditions improve, the surviving meristems can generate new leaves if the adult leaves are dead (Van Peer et al., 2004; Zwicke et al., 2015). In some species and genotypes from very dry areas, survival of basal meristematic tissues is achieved through summer dormancy (Volaire and Norton, 2006). In these plants, photoperiod and temperature induce (even under irrigation) cessation or reduction of shoot growth, various degrees of foliage senescence and a dehydration tolerance of meristems. The reduction in leaf tissue reduces total plant water loss (Gepstein, 2004; Munne Bosch and Alegre, 2004). A minimum water supply to the meristematic tissues is maintained (Karcher et al., 2008; McWilliam and Kramer, 1968; Volaire and Lelievre, 2001), and high concentrations of fructans and dehydrins contribute to osmoregulation and membrane stabilisation of these tissues (Hincha et al., 2000, 2002). High carbohydrate reserves are associated with superior plant resilience and recovery after severe drought (Boschma et al., 2003). Thus, to interpret low leaf water potential or high foliage senescence as responses associated with drought sensitivity and poor adaptation may be correct if maintained production under drought is the target, but highly misleading if drought survival during severe drought is the focus. Making the distinction between the responses of mature and young meristematic tissues is crucial when analysing the strategies of perennial grasses to contrasting drought intensities. It may be possible to combine drought resilience of perennial forage species with high biomass productivity in rainy seasons, as recently shown by crossing summer dormant with summer active and highly productive genotypes of cocksfoot (Kallida et al., 2016). Breeding programs are now starting to focus on the improvement of drought survival instead of targeting the maintenance of growth under moderate drought (Volaire et al., 2014). A broadening of the gene pools of most of the currently used species is probably necessary (Mäkinen et al., 2016), and future breeding, irrespective of crop species, demands efficient ways to incorporate wild adapted genetic resources and exotic material into the current breeding base (Helgadóttir et al., 2014). As argued above, the use of forage legumes has many advantages including nitrogen fixation, utilization of elevated CO_2 and improvement of forage quality. In spite of this, there are only a few species used in the Nordic region, and the breeding efforts in the Mediterranean region have been limited. Many annual and perennial legume species, and their rhizobial symbionts, have been collected and developed into varieties and rhizobial strains now widely used in Mediterranean climates in Australia (Nichols et al., 2012). This suggests that varieties of a larger number of legume species could also be developed for use in different regions of Europe. Interestingly, although the Nordic and Mediterranean regions of Europe represent very different climates, there is some common ground in the adaptation of perennial grassland species to these climates: (i) seasonal regulation of growth and dormancy or quiescence, whether it is the winter or the summer that needs to “be survived”, are likely to be regulated by similar molecular signalling systems responding to temperature and photoperiod (Gillespie and Volaire, 2017; Ergon, 2017), and (ii) tolerance of the tissue to seasonal stresses, whether it is freezing or drought, is partly based on the same mechanisms, both regarding induction of tolerance and the protective mechanisms themselves (Dolferus, 2014).

3.3. Adapting grassland management

The expected increase in rate of phenological development, and in some cases productivity, requires adaptation of defoliation and fertilization regimes. Moreover, in grasslands, the constraints on utilization of the CO_2 fertilizing effect caused by photosynthetic acclimation can largely be overcome through defoliation (maintaining sink strength)

and use of legumes (maintaining N availability), provided that there are sufficient amounts of water and other nutrients available (Soussana and Hartwig, 1996; Rogers et al., 1998; Picon-Cochard et al., 2004). Höglind et al. (2013) predicted that the earlier spring and higher temperatures would allow for one more cut per growing season in Northern Europe during the future period 2040–2065 compared to 1961–1990. In an attempt to reduce costs linked to an extra cut, farmers may decide to increase grazing. However, as N use efficiency of swards can be considerably lower under grazing compared to cutting (Nevens and Reheul, 2003), and as climate change is expected to create a higher potential for leaching in grazed grassland compared to cut grassland (Saarijärvi et al., 2004; Stuart et al., 2011), N fertilization has to be judiciously adjusted to prevailing management practices and climatic conditions in grazed systems to avoid excessive N leaching. In the current Nordic climate, excessive precipitation frequently causes problems with farm operations (Peltonen-Sainio et al., 2009; Olesen et al., 2011). Increased precipitation and waterlogged soils could make establishment of new leys, application of fertilizer, and harvesting challenging in some years, and is likely to increase nutrient runoff during winter (Saarijärvi et al., 2007; Edwards et al., 2007; Deelstra et al., 2011). With increased precipitation levels, care is needed to minimize soil compaction during farm operations, and maintain or improve drainage systems, particularly on some soil types (Rivedal et al., 2016). In the driest Mediterranean semi-natural grasslands dominated by annual species, grazing by livestock is recognized as the main driver influencing vegetation dynamics, species diversity and grassland productivity (Köchy et al., 2008; Carmona et al., 2012; Sternberg et al., 2015), and thus needs to be managed carefully, e.g. through the use of flexible stocking (Pahl et al., 2016). Similarly, the persistence of perennial forage species during a severe drought is affected by the defoliation regime in spring (Boschma et al., 2003) which can be detrimental if too intense, to the accumulation of water soluble carbohydrates ensuring drought survival of meristematic tissues (Volaire, 1994; Volaire and Gandoin, 1996). The exploitation of alternative forage resources in wooded grasslands could be a strategy to cope with the foreseen reduced pasture production (Moreno and Pulido, 2009; Del Prado et al., 2014). Such alternative forages may include tree leaves and shrubs, which can alleviate feed shortages, or even fill feed gaps in the winter and especially in the summer in small-scale livestock farms in dry to semi-arid climates (Papanastasis et al., 2008).

4. Conclusions and perspectives for research priorities

Climate change can increase grassland productivity due to higher temperatures, longer growing seasons and higher CO_2 concentration, if there is sufficient amount of water available. However, water limitation will occur increasingly, particularly in the Mediterranean region during summer. Water limitation of forage production can to some extent be alleviated by higher CO_2 concentration, which increases the water use efficiency, and by a shift in productivity towards the cooler part of the year in Mediterranean climates. The effect of climate change on plant winter survival in the Nordic region is difficult to predict due to interactions between temperature and snow cover on winter stress levels, and the interactions between temperature and light factors on cold acclimation and deacclimation processes. Other uncertainties regarding increased forage production in the Nordic region in the future climate includes water saturated soils and soil compaction, practical problems with cultivation and harvesting, and increasing occurrence of weeds, pests and diseases. Climate change can affect forage quality in several ways in both Nordic and Mediterranean regions through its effects on plant growth and development as well as species composition.

In the face of unstable and uncertain climatic conditions, a high diversity of cultivated forage species, high intraspecific genetic diversity, and the use of species and variety mixtures can enhance productivity and resilience of grasslands. In both the Mediterranean and Nordic regions, climate change will lead to changes in the annual growth patterns of grassland species (both growth rates and timing of growth), prompting adaptations of fertilization and defoliation regimes (timing and intensity). Breeding and research efforts should be stimulated towards (i) improving plant strategies to cope with relevant stresses in appropriate ways (e.g. maintenance of growth under moderate stress and survival under severe stress), (ii) optimizing the regulation of growth so that it fits new seasonal climate and defoliation patterns (e.g. increase growth potential during the cooler part of the year in the Mediterranean region or during spring in the Nordic region, and improve regrowth capacity after defoliation in the Nordic region), and (iii) utilizing plant diversity at all levels (e.g. develop mixtures with inter- and intraspecific variation in responses to climatic variables).

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