1   How can forage production in Nordic and Mediterranean Europe adapt to the challenges and

2   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.

Keywords: breeding, forage, management, persistence, productivity, seasonal stress

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; 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

68   become 1-3 months longer by the end of the century as compared to the period 1971-2000

69   (Ruosteenoja *et al.*, 2011; Hanssen-Bauer *et al.*, 2015). Annual precipitation in the Nordic region

70   is predicted to increase considerably (up to around 20 % relative to 1971-2000 in some regions)

71   by the end of the century, with more frequent episodes of extreme precipitation, and especially

72   during winter (Lehtonen *et al.*, 2014; Hanssen-Bauer *et al.*, 2015). In the Mediterranean region,

73   the climate is expected to become warmer and drier, particularly in summer (Giorgi and

74   Lionello, 2008; Giannakopoulos *et al.*, 2009; Lehtonen *et al.*, 2014). Winters are also expected to

75   become warmer, but to a lesser extent than summers, while winter precipitation may vary

76   between regions (Giorgi and Lionello, 2008; Giannakopoulos *et al.*, 2009; Hoerling *et al.*, 2012).

77   Increased inter-annual variability in summer and winter precipitation, as well as in summer

78   temperatures, is also expected (Giorgi and Lionello, 2008). Changes in atmospheric CO_2

79   concentration, temperature and precipitation patterns are expected to affect plant productivity in

80   a complex manner due to a set of mechanisms and interactions at different scales from the

81   individual leaves to agroecosystems (Hatfield and Prueger, 2010; Xu *et al.*, 2013). For

82   grasslands, there are also important complicating factors such as plant competition and other

83   plant-plant interactions, perennial growth habits, seasonal productivity patterns, and plant-animal

84   interactions (Porter *et al.*, 2014).

85

86   Grasslands comprise a variety of vegetation types and management systems (e.g. Allen *et al.,*

87   2011; Huyghe *et al.,* 2014; Peeters *et al.*, 2014). A distinction is made between temporary and

88   permanent grasslands. Temporary grasslands, also termed forage crops, are regularly re-

89   established (annually or at longer intervals), or constitute an element in a crop rotation.

90   Permanent grasslands are grasslands that have either never been ploughed or not been ploughed

91 for at least five to ten years (definitions vary). Permanent grasslands can range from natural and

92 semi-natural (not managed by other means than grazing or mowing) to agriculturally improved

93 permanent grasslands (i.e. improved by fertilization). Both temporary and permanent grasslands

94 may be harvested by mowing (meadows), grazing (pastures) or a combination, and consist of

95 perennial, biennial and/or annual forage species, mainly grasses and legumes. Overviews of

96 grassland production in the Nordic and Mediterranean regions of Europe were recently given by

97 Helgadóttir *et al.* (2014) and Porqueddu *et al.* (2016). Nordic grasslands are dominated by

98 perennial grasses, with a few perennial legume species also present. Annual species are used

99 only to a limited extent. There are both permanent and temporary grasslands, which are grazed or

100 mown. Due to the lack of plant growth during winter, there is a strong reliance on harvested and

101 conserved forage. In Mediterranean Europe, grasslands can be grazed from autumn to spring and

102 may be mown in spring for hay production. Permanent grasslands can be dominated both by

103 perennial and annual grasses, while temporary grasslands are often dominated by annual species.

104 In summer, forage production can be completely or very limited by drought. Agro-silvopastoral

105 systems are important in some areas. Annual and perennial grasses and legumes such as alfalfa

106 (*Medicago sativa* L.) are to some extent cultivated as forage crops, which are sometimes

107 irrigated. We here review the current research available related to the challenges and

108 opportunities for forage production associated with changing climate in these two contrasting

109 regions. We consider challenges and opportunities created by climate change in terms of forage

110 productivity, forage quality and plant species composition (Section 2), while also assessing how

111 utilization of plant traits and management practices could enable adaptation (Section 3).

112 Although intimately linked to forage production, livestock production and the integration of

113 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

136 becomes a restricting factor for growth, particularly at higher latitudes (Ruosteenoja and

137 Räisänen, 2013, Uleberg *et al.*, 2014; Virkajärvi *et al.*, 2015).

138

139 There are many uncertainties regarding winter stresses in a future climate (Rapacz *et al.*, 2014).

140 The type and severity of winter stresses depends not only on the minimum temperature during

141 winter, but also largely on the presence or absence of a snow cover, and on factors that control

142 the cold acclimation status of the plants. Decrease in long-term mean snowpack has been

143 predicted toward the end of the century, although individual snow-rich winters will still occur

144 (Räisänen and Eklund, 2011). Thus, there will be shorter duration of snow cover and eventually

145 snow-free winters in some regions now characterized by stable snow cover. On the other hand,

146 increased precipitation in areas where temperatures remain below freezing can give longer-

147 lasting snow cover in some areas (Johansson *et al.*, 2011). Less snow cover can increase the

148 occurrence, depth and duration of soil frost due to less insulation (Kellomäki *et al*. 2010; Bjerke

149 *et al.*, 2015), and was shown to affect annual productivity of grasslands in Canada and Germany

150 (Vankoughnett *et al*., 2016; Zeeman *et al.,* 2017). There has been an increase in frequency of

151 winter warming events in northern Norway, Sweden, and Finland during the last 50 years

152 (Vikhamar-Schüler *et al*., 2016). This has led to increased numbers of melt-days during winter

153 by 3-7 days per decade, and a further increase in such events are projected. The combination of

154 increased precipitation in the autumn and winter, milder and unstable temperatures, and frozen

155 soils, may lead to ice cover or waterlogging. The risk of winter damage is expected to increase

156 east of the Baltic Sea, even for the winter hardy species timothy, while the risk of spring frost

157 damage is predicted to increase in the western part of the Nordic area (Höglind *et al*., 2013). In

158 winter, when solar irradiation is insufficient for photosynthesis in northern latitudes, the carbon-

159 economy and survival of the plants becomes increasingly important when temperatures exceed

160 $5^{o}C$ and respiration increases. On the other hand, if temperatures remain cool, shorter winters

161 could leave more C and N reserves in spring, increasing survival and spring DM production (Jing

162 *et al.*, 2013; Piva *et al.*, 2013). Higher temperatures in autumn will shift cold acclimation of the

163 plants to a time when less light is available. This can have impacts on growth cessation and cold

164 acclimation of plants (Østrem *et al.,* 2014; Dalmannsdottir *et al.*, 2017, Ergon 2017), rendering

165 them more vulnerable to winter stresses. In addition, waterlogged soils in combination with

166 higher autumn temperatures have negative effects on cold acclimation of timothy (Jørgensen *et*

167 *al.*, 2016). Unstable winter temperatures and early springs can cause plants to de-acclimate,

168 when there is still a risk of freezing (Jørgensen *et al.*, 2010; Rapacz *et al.*, 2014). The distribution

169 of many weeds, pests and pathogens are limited to the north by harsh winters. With global

170 warming, many of these species can be expected to spread northward (Jepsen *et al.,* 2011;

171 Juroszek and von Tiedemann, 2013; Svobodová *et al.*, 2014).

172

173 More severe and frequent droughts leading to reduced productivity through both reduced growth

174 and reduced persistence, is considered the major climate challenge for forage production in the

175 Mediterranean region in the future. The direct effect of heat stress is not likely to be of the same

176 importance in grasslands as in grain crops, where heat stress during certain stages of

177 reproductive development can be detrimental for yields. In the Mediterranean region, water

178 availability will often be more limiting for photosynthesis than the atmospheric CO_2

179 concentration, but CO_2 concentration still has important effects due to interactions with

180 temperature and drought. Elevated CO_2 can partly compensate for the reduced CO_2 influx

181 through stomata under moderate drought (Ainsworth and Long, 2005; Soussana *et al.,* 2010).

182 Consequently, elevated CO_2 enhances biomass production and improves water relations under

183 drought (Clark *et al.*, 1999). In addition, elevated CO_2 contributes to water sparing (reduced

184 transpiration due to less stomatal opening) during periods when sufficient water is available,

185 leaving more water for later in the season, when the water reserves might otherwise be exhausted

186 (Morgan *et al.,* 2004).

187

188 In Mediterranean Europe, the productivity of rainfed grasslands is limited during the dry

189 summer. Changes in the seasonal patterns of temperature and precipitation are likely to shift

190 productivity further towards cooler and wetter parts of the year. Projections of climate change

191 impact on grassland productivity (Graux *et al*., 2013) indicated that summer yields may be

192 reduced in Mediterranean France in the far future (2070-2099). However, in this study higher

193 yields were predicted in autumn, winter and spring due to a combined effect of higher

194 temperatures and CO_2 levels, leading to an overall increase in productivity. In line with this,

195 Dono *et al.* (2016), modelling productivity of semi-natural grasslands dominated by self-

196 reseeding annual species (no summer production) in the near future (2020-2030) in Sardinia,

197 Italy, predicted decreased spring yields and higher autumn yields due to increased temperature

198 and increased rainfall occurrence in October. In the same study, irrigated annual ryegrass crops

199 were predicted to have increased yields in the near future. Model-based studies are affected by

200 uncertainties and assumptions and, as Graux *et al.* (2013) pointed out, their study neither

201 accounted for a possible increase in mortality of perennials during summer droughts, nor climate

202 change-induced changes in species composition, both factors that may have importance in

203 grasslands.

204

205   In summary, grassland productivity can be expected to increase in the Nordic region, and shift

206   towards winter in the Mediterranean region, except on relatively moist or irrigated land (Table 1,

207   Fig. 1).

208

209   2.2. Forage quality and species composition

210   Climate change may affect forage quality in different ways. Higher temperatures lead to earlier

211   stem elongation, a faster rate of decline in cell wall digestibility of both vegetative and

212   reproductive tillers during aging, and hence faster decline in the digestibility of forages (Groot *et*

213   *al.,* 2003; Thorvaldson *et al.*, 2007; Bertrand *et al.*, 2008; Bloor *et al.*, 2010; Jing *et al*., 2013). In

214   addition, higher standing biomass is associated with higher stem-to-leaf proportions and lower

215   digestibility, at least in timothy (Bélanger and McQueen 1998; Bélanger *et al*., 2001), and thus

216   climate change may lead to lower or higher digestibility through its effect on growth rate, stand

217   density and competition for light. The effects of phenological development and standing biomass

218   can largely be compensated by changes in defoliation regimes and fertilization (discussed

219   below). Climate change may also affect forage quality through effects on species composition.

220   Elevated CO_2 tends to increase the competitive ability of legumes in legume-grass mixtures, if

221   the legumes are not limited by minerals such as phosphorous (reviewed by Lüscher *et al.,* 2004;

222   Soussana and Lüscher, 2007; Soussana *et al.,* 2010). This may compensate for the slight decrease

223   in protein content of grasses at elevated CO_2 (Soussana and Lüscher, 2007; Dumont *et al.*, 2015).

224   Dumont *et al.* (2015), in their meta-study of climate change effects on forage quality, found that

225   elevated CO_2 did not affect digestibility, but increased the total non-structural carbohydrate

226   content by an average of 25 % and decreased N content by 8 %, reflecting the shift in the C:N-

227   ratio of the environment. N content increased with increasing drought level, and unlike other

228   sites, a decrease in herbage N concentration in response to elevated CO_2 was not found at

229   Mediterranean sites. The authors suggested that this could be due both to water limitation on

230   growth, and changes in species composition (higher legume proportion), leading to higher

231   concentration of N in the forage. In some Mediterranean regions, e.g. in semi-arid Italy, semi-

232   natural grasslands are dominated by annual species that are maintained by seed banks (Cosentino

233   *et al.,* 2014). The species composition in these grasslands varies between years, depending on

234   previous seed production, dormancy and germination. These are all processes strongly

235   influenced by climatic conditions such as temperature and moisture, and therefore most likely

236   affected by climate change (Ooi, 2012; Cosentino *et al.,* 2014; Long *et al.,* 2015).

237   3. How to address these challenges and opportunities?

238   Grassland management targets an optimal balance between forage yield, forage quality, yield

239   stability and persistence (plant survival or reproduction). This can be achieved through a suitable

240   choice of plant material, optimization of the defoliation and fertilization strategies, irrigation,

241   drainage, soil management, control of unwanted organisms, and renovation or re-establishment

242   of the grassland.

243

244   3.1. Choice of plant material

245   Choosing the best species and mixtures for sown grasslands can be a way to meet challenges and

246   utilize opportunities raised by climate change. A harsh winter climate is the strongest limiting

247   factor determining which perennial species can be cultivated in the Nordic region. Although

248   there is considerable uncertainty regarding winter survival in the future, a longer growing season

249   and milder winters may increase the prospective for using species and cultivars with higher yield

250 potential and feeding value. Currently, winter hardy species such as timothy, meadow fescue

251 (*Schedonorus pratensis* Huds. syn. *Festuca pratensis* Huds.) and red clover (*Trifolium pratense*

252 L.), are widely used (Helgadottir *et al.*, 2014). Species like perennial ryegrass (*Lolium perenne*

253 L.) and festulolium (×*Festulolium* Aschers. et Graebn.) are used in the southern Nordic area, and

254 are of increased interest for the future climate also further north because of their high production

255 capacity throughout the growing season as well as high nutritive value (Østrem *et al.,* 2013).

256 Including deep-rooted drought tolerant species like tall fescue (*S. arundinaceus* Schreb. *syn. F.*

257 *arundinacea* Schreb.), fescue type festulolium, cocksfoot (*Dactylis glomerata* L.), red clover and

258 lucerne in the mixtures can be a strategy to prevent yield reduction during drought periods. Tall

259 fescue has a better nitrogen uptake, nitrogen use efficiency and water use efficiency, and a yield

260 potential which is up to 50 % higher than perennial ryegrass in dry periods, most probably owing

261 to its deeper rooting system (Cougnon, 2013; Cougnon *et al*., 2017). In addition, it can tolerate

262 poorly drained soils (Barnes *et al.,* 2003). However, the digestibility and animal preference is

263 lower than in perennial ryegrass (Cougnon *et al.*, 2014). Cultivation of whole crop maize (*Zea*

264 *mays* L.) has increased during the last decades and the expected climate changes will further

265 promote this development, at least in southern parts of the Nordic region (Elsgaard *et al.*, 2012).

266 This could be compatible with an increased use of legumes and total mixed ratio feeding

267 strategies, where high protein forages can be complemented with low protein but high energy

268 components, and thereby influencing what type of grasslands will be cultivated.

269

270 A wide range of annual forage species showing adaptability to Mediterranean climate conditions

271 are currently available in the market (e.g. oat (*Avena sativa* L.), italian ryegrass (*L. multiflorum*

272 Lam.), crimson clover (*T. incarnatum* L.), egyptian clover (*T. alexandrinum* L.), common vetch

273 (*Vicia sativa* L.)) (Annicchiarico *et al.,* 2013; Porqueddu *et al*., 2016). Despite an increasing use

274 of annual self-reseeding species (mainly subterranean clover (*T. subterraneaum* L.) and

275 *Medicago* spp.) for pasture improvement in dry environments (Porqueddu and Gonzalez, 2006),

276 cultivars available in the seed market have often proved to be poorly adapted to the climatic

277 conditions and management systems of Mediterranean Europe (Sulas, 2005; Salis *et al*., 2012;

278 Porqueddu *et al*., 2016). Native genotypes of these species (e.g., rigid ryegrass (*L. rigidum*

279 Gaud.) and burr medic (*M. polymorpha* L.)) have been selected (Porqueddu *et al*., 2001; Franca

280 *et al.,* 2005), but not adopted by the seed industry in Europe so far. Perennial forages such as tall

281 fescue or cocksfoot can be a valuable alternative to annuals, if they can survive across successive

282 summer droughts. Although most of the temperate origin cultivars available on the market are

283 not drought persistent in Mediterranean areas (Lelièvre and Volaire 2009), a few cultivars with

284 summer dormancy (Volaire and Norton, 2006) can tolerate severe successive droughts and

285 survive in environments with annual rainfall as low as 300 mm (Annichiarico *et al.,* 2011;

286 Pecetti *et al.,* 2009, 2011). Under chronic water shortages, perennial forage species have a

287 number of advantages in comparison to the predominantly used annual species including (i)

288 fewer inputs with less field preparation and fertilizer requirement, (ii) year-around soil cover

289 reducing the risk of intense soil erosion, (iii) optimal use of water throughout all seasons, thus

290 enhancing forage production in particular in autumn when cereals and annual species are not yet

291 established and (iv) greater flexibility because of the multiple uses of these species (grazing, hay,

292 silage). Therefore, perennial species are an excellent alternative to annual species, contributing to

293 reduced production costs, to halt rangeland degradation and overall to confer greater security to

294 rain-fed agricultural systems (Lelièvre and Volaire, 2009; Volaire *et al.,* 2016). Cultivars of

295 bulbous canary-grass (*Phalaris aquatica* L.) and tall fescue that express summer dormancy play

296   an increasing role in eastern Australia and the semi-arid environment of the Southern Great

297   Plains in the USA, and can be used in regions with down to about 550 -500 mm precipitation per

298   year (Oram and Lodge, 2003; Malinowski *et al.,* 2005, 2009¸ Norton *et al.,* 2016). Such cool

299   season grasses were also found to be quite productive and successful in south-west Australia

300   (Rogers et al., 1976; Biddiscombe et al., 1977) although until recently they have been poorly

301   adopted by the seed industry. The association of summer dormant grasses and Mediterranean

302   type alfalfa, combining the dehydration tolerance of the grass and the dehydration avoidance of

303   the legume provides high functional complementarity for water use in summer and is advocated

304   for drought prone areas (Volaire *et al.,* 2016).

305

306   Unstable conditions with large variation in weather within and between seasons increase

307   uncertainty in forage production. Diversity among responses to critical weather factors improves

308   resilience at both sward and farm level (Mäkinen *et al.*, 2015). Seed and variety mixtures with

309   components that have both desired traits and complementary niches can exploit temporal and

310   spatial variation in environmental conditions, and be more stable and robust compared to

311   monocultures or simple mixtures. Using mixtures is therefore considered a key strategy to

312   maintain production in unpredictable and unstable environments (Maltoni *et al.,* 2007; Volaire *et*

313   *al.,* 2014; Lüscher *et al*., 2014). Species and variety mixtures also tend to be more stable in

314   forage quality than pure stands of one species (Sleugh *et al.,* 2000; Sanderson, 2010; Ergon *et*

315   *al.,* 2016), and therefore allows for some flexibility in harvest times, which is desirable in rainy

316   summers in the Nordic region. It may be possible to design optimized mixture compositions

317   based on detailed experiments (Goslee *et al*., 2013). For example, mixtures of summer-dormant

318   and summer-active perennial species may provide stable pastures exploiting available soil

319   moisture throughout the year in some Mediterranean regions (Norton *et al.,* 2016). Similarly,

320   grass-legume mixtures including both annuals and perennials proved to achieve higher yields and

321   utilize a longer period for growth than pure stands, under dry Mediterranean conditions

322   (Porqueddu and Maltoni, 2007; Maltoni *et al.,* 2007). However, when a single environmental

323   factor is dominant, yield and survival may depend largely on a specific trait rather than on

324   functional diversity. For example, under severe summer water deficit, rooting depth enhanced

325   water uptake and resilience of grass communities irrespectively of the level of species diversity

326   in the communities (Barkaoui et al., 2016). Including N-fixing legumes in mixtures has several

327   advantages, and can facilitate a better exploitation of elevated atmospheric CO_2 concentration

328   (Lüscher *et al.,* 2004, 2014). However, since legumes require relatively high amounts of K and

329   P, nodulation and N fixation may become limited by low nutrient supply and high or low

330   temperatures (Nesheim and Boller, 1991; Irigoyen *et al.,* 2014), and the conservation of legume

331   forage can be challenging, particularly in a wet Nordic climate.

332

333   3.2 Breeding for the future climate

334   In order to meet the challenges and utilize the opportunities that climate change will bring, the

335   plant material we cultivate should (i) exhibit growth cycles that better fit the new seasonal

336   climate patterns, (ii) be able to cope with relevant stresses and have the right balance between

337   growth potential, nutritive value and stress tolerance, and (iii) have the phenotypic plasticity or

338   genetic diversity within populations that ensures yield stability under variable and unpredictable

339   conditions.

340

341 The annual recurrent periods of winter stresses or summer droughts have led to the evolution of

342 seasonal acclimation and de-acclimation processes regulating the level of resistance to seasonal

343 stresses in perennial grasses (Laude, 1953, Volaire and Norton, 2006, Preston and Sandve,

344 2013). These processes, which are largely regulated by temperature and photoperiod, correlate

345 with changes in growth, reproductive development and dormancy status (Preston and Sandve,

346 2013, Norton *et al.,* 2009, Gillespie and Volaire, 2017), and latitudinal clines in responses to

347 temperature and photoperiod have been described (Cooper, 1964). With global warming, there

348 will be new combinations of temperature and photoperiod. This is particularly the case in the

349 north where photoperiod changes dramatically during the course of a year. In order to utilize a

350 longer growing season in Nordic Europe, and a shift in the growing season in Mediterranean

351 Europe, we need species and varieties with temperature and photoperiod responses conferring an

352 annual growth pattern that optimizes growth during the favourable part of the year and survival

353 during the cold Nordic winter or dry Mediterranean summer (Ergon, 2017). Resistance to winter

354 stresses are still likely to be of high importance in the Nordic region in the future (see section 1).

355 Plants encounter many stresses during winter: freezing, anoxia due to ice encasement or water-

356 saturated soils, soil movements due to freeze-thaw cycles, winter pathogens, starvation and

357 dehydration due to frozen soils. Specific resistance mechanisms to these stresses exist, but they

358 are also largely interconnected through genetics and physiology. Central to winter survival is

359 proper cold acclimation in autumn and sufficient maintenance of a cold acclimated state in

360 spring. During cold acclimation, leaf elongation ceases, a number of stress responses are elicited,

361 and organic reserves accumulate. Both cold acclimation in autumn and deacclimation in spring

362 are mainly controlled by temperature. However, light is also important in at least three different

363 ways: (i) high irradiance combined with low temperature increases the photosystem II excitation

364   pressure, eliciting signalling pathways leading to cold acclimation, (ii) light is the energy source

365   for the accumulation of organic reserves, and (iii) photoperiod is a developmental signal

366   influencing growth, cold acclimation and deacclimation. Due to these reasons, the shift of cold

367   acclimation and deacclimation into shorter photoperiods may affect the ability of plants to cope

368   with winter stresses (Dalmannsdottir *et al.,* 2017). A more detailed and quantitative

369   understanding of interactions between temperature and light on winter survival in different

370   species is needed. Breeding activities may need to focus on adjusting the timing of growth

371   cessation and cold acclimation in autumn, and the opposite process in spring, to new temperature

372   and photoperiod combinations. For example, at high latitudes, perennial ryegrass and festulolium

373   tend to cease growth in autumn too late for sufficient cold acclimation (Østrem *et al.*, 2014). It

374   will however, be necessary to manage the trade-off between optimal timing with respect to

375   winter survival, and utilization of the longer growing season to increase production (Ergon,

376   2017). In order to utilize the potential for higher productivity in the north, there is also a need for

377   strong regrowth capacity and tolerance to more frequent harvesting or grazing. For timothy, the

378   priorities would likely be to improve tolerance to harvesting and grazing, better regrowth

379   capacity and spring growth. Perennial ryegrass needs better winter survival, particularly

380   improved timing of growth cessation and cold acclimation, as well as resistance to psycrophilic

381   pathogenic fungi (Abdelhalim *et al*., 2016), while for tall fescue, work is ongoing to combine the

382   high yield and drought tolerance with an acceptable digestibility and animal preference

383   (Humphreys *et al.*, 2012, Helgadottir et al., 2014, Cougnon *et al.*, 2015; Fariaszewska *et al.*,

384   2016).

385

386 Drought escape (i.e. when plants survive the dry summer as seeds; Long *et al.,* 2015) and

387 hardseededness (which allows a more persistent seed bank; Taylor, 2005) are the main adaptive

388 strategies of annual species in Mediterranean grasslands. Based on the predicted changes in

389 precipitation, with an overall reduced growth period in the driest Mediterranean regions, annual

390 species will need earlier seed maturation for reliable seed set in shorter growing seasons, as well

391 as mechanisms (i.e. regulation of seed dormancy and germination) ensuring the presence of a

392 seedbank under the expected seasonal patterns of temperature and water availability (Porqueddu

393 *et al.,* 2016). A low requirement for dormancy release gives the potential for early germination

394 and higher yield, but at the risk of seedling mortality due to false breaks. Given the uncertainty

395 and the expected climatic variability, intra- and interspecific variation in regulation of dormancy

396 release in cultivars and seed mixtures appears to be a good strategy. In the past, breeding efforts

397 in tall fescue and cocksfoot have mainly been directed towards use in temperate areas with

398 summer active material that are short lived under drought, and there are therefore very few

399 cultivars adapted to severe drought currently available in southern Europe (Lelièvre and Volaire,

400 2009). Persistence during severe drought is governed by mechanisms different from those

401 conferring resistance to moderate droughts (Milbau *et al.*, 2005; Volaire *et al.*, 2009). Plants with

402 responses resulting in resistance under moderate drought and maintenance of shoot growth have

403 to either avoid or tolerate leaf dehydration. At moderate drought, the maintenance of biomass

404 production can be achieved primarily by maximizing soil water capture while maintaining

405 stomatal gas exchange and transpiration (Blum, 2009). A deep root system with a high density of

406 roots at depth (Carrow, 1996; Wasson *et al.*, 2012; White and Snow, 2012) and maintenance of

407 leaf area, leaf relative water content, leaf cell turgor and photosynthetic capacity (Morgan, 1988;

408 Serraj and Sinclair, 2002) are traits that are associated with high yield in water-limited

409   environments. Plant responses resulting in survival under severe drought, however, are mainly

410   associated with growth cessation, dehydration avoidance and tolerance occurring in young

411   tissues including basal meristematic tissues. When conditions improve, the surviving meristems

412   can generate new leaves if the adult leaves are dead (Van Peer *et al.,* 2004; Zwicke *et al.*, 2015).

413   In some species and genotypes from very dry areas, survival of basal meristematic tissues is

414   achieved through summer dormancy (Volaire and Norton, 2006). In these plants, photoperiod

415   and temperature induce (even under irrigation) cessation or reduction of shoot growth, various

416   degrees of foliage senescence and a dehydration tolerance of meristems. The reduction in leaf

417   tissue reduces total plant water loss (Gepstein, 2004; Munne Bosch and Alegre, 2004). A

418   minimum water supply to the meristematic tissues is maintained (Karcher *et al*., 2008;

419   McWilliam and Kramer, 1968; Volaire and Lelievre, 2001), and high concentrations of fructans

420   and dehydrins contribute to osmoregulation and membrane stabilisation of these tissues (Hincha

421   *et al.*, 2000; 2002). High carbohydrate reserves are associated with superior plant resilience and

422   recovery after severe drought (Boschma *et al.*, 2003). Thus, to interpret low leaf water potential

423   or high foliage senescence as responses associated with drought sensitivity and poor adaptation

424   may be correct if maintained production under drought is the target, but highly misleading if

425   drought survival during severe drought is the focus. Making the distinction between the

426   responses of mature and young meristematic tissues is crucial when analysing the strategies of

427   perennial grasses to contrasting drought intensities. It may be possible to combine drought

428   resilience of perennial forage species with high biomass productivity in rainy seasons, as recently

429   shown by crossing summer dormant with summer active and highly productive genotypes of

430   cocksfoot (Kallida *et al.,* 2016). Breeding programs are now starting to focus on the

431   improvement of drought survival instead of targeting the maintenance of growth under moderate

432   drought (Volaire *et al.,* 2014). A broadening of the gene pools of most of the currently used

433   species is probably necessary (Mäkinen *et al*., 2016), and future breeding, irrespective of crop

434   species, demands efficient ways to incorporate wild adapted genetic resources and exotic

435   material into the current breeding base (Helgadóttir *et al.*, 2014). As argued above, the use of

436   forage legumes has many advantages including nitrogen fixation, utilization of elevated CO_2 and

437   improvement of forage quality. In spite of this, there are only a few species used in the Nordic

438   region, and the breeding efforts in the Mediterranean region have been limited. Many annual and

439   perennial legume species, and their rhizobial symbionts, have been collected and developed into

440   varieties and rhizobial strains now widely used in Mediterranean climates in Australia (Nichols

441   *et al.,* 2012). This suggests that varieties of a larger number of legume species could also be

442   developed for use in different regions of Europe. Interestingly, although the Nordic and

443   Mediterranean regions of Europe represent very different climates, there is some common

444   ground in the adaptation of perennial grassland species to these climates: (i) seasonal regulation

445   of growth and dormancy or quiescence, whether it is the winter or the summer that needs to "be

446   survived", are likely to be regulated by similar molecular signalling systems responding to

447   temperature and photoperiod (Gillespie and Volaire, 2017; Ergon, 2017), and (ii) tolerance of the

448   tissue to seasonal stresses, whether it is freezing or drought, is partly based on the same

449   mechanisms, both regarding induction of tolerance and the protective mechanisms themselves

450   (Dolferus, 2014).

451

452   3.3. Adapting grassland management

453   The expected increase in rate of phenological development, and in some cases productivity,

454   requires adaptation of defoliation and fertilization regimes. Moreover, in grasslands, the

455   constraints on utilization of the CO_2 fertilizing effect caused by photosynthetic acclimation can

456   largely be overcome through defoliation (maintaining sink strength) and use of legumes

457   (maintaining N availability), provided that there are sufficient amounts of water and other

458   nutrients available (Soussana and Hartwig, 1996; Rogers *et al*., 1998; Picon-Cochard *et al.,*

459   2004). Höglind *et al.* (2013) predicted that the earlier spring and higher temperatures would

460   allow for one more cut per growing season in Northern Europe during the future period 2040-

461   2065 compared to 1961-1990. In an attempt to reduce costs linked to an extra cut, farmers may

462   decide to increase grazing. However, as N use efficiency of swards can be considerably lower

463   under grazing compared to cutting (Nevens and Reheul, 2003), and as climate change is expected

464   to create a higher potential for leaching in grazed grassland compared to cut grassland (Saarijärvi

465   *et al*., 2004, Stuart *et al.,* 2011), N fertilization has to be judiciously adjusted to prevailing

466   management practices and climatic conditions in grazed systems to avoid excessive N leaching.

467   In the current Nordic climate, excessive precipitation frequently causes problems with farm

468   operations (Peltonen-Sainio *et al.*, 2009, Olesen *et al.*, 2011). Increased precipitation and

469   waterlogged soils could make establishment of new leys, application of fertilizer, and harvesting

470   challenging in some years, and is likely to increase nutrient runoff during winter (Saarijärvi *et*

471   *al.,* 2007, Edwards *et al*., 2007; Deelstra *et al*., 2011). With increased precipitation levels, care is

472   needed to minimize soil compaction during farm operations, and maintain or improve drainage

473   systems, particularly on some soil types (Rivedal *et al.,* 2016). In the driest Mediterranean semi-

474   natural grasslands dominated by annual species, grazing by livestock is recognized as the main

475   driver influencing vegetation dynamics, species diversity and grassland productivity (Köchy *et*

476   *al.,* 2008; Carmona *et al.,* 2012; Sternberg *et al.,* 2015), and thus needs to be managed carefully,

477   e.g. through the use of flexible stocking (Pahl *et al.,* 2016). Similarly, the persistence of

478   perennial forage species during a severe drought is affected by the defoliation regime in spring

479   (Boschma *et al.,* 2003) which can be detrimental if too intense, to the accumulation of water

480   soluble carbohydrates ensuring drought survival of meristematic tissues (Volaire, 1994; Volaire

481   and Gandoin, 1996). The exploitation of alternative forage resources in wooded grasslands

482   could be a strategy to cope with the foreseen reduced pasture production (Moreno and Pulido,

483   2009; Del Prado *et al.,* 2014). Such alternative forages may include tree leaves and shrubs, which

484   can alleviate feed shortages, or even fill feed gaps in the winter and especially in the summer in

485   small-scale livestock farms in dry to semi-arid climates (Papanastasis *et al.,* 2008).

4. Conclusions and perspectives for research priorities

487   Climate change can increase grassland productivity due to higher temperatures, longer growing

488   seasons and higher CO_2 concentration, if there is sufficient amount of water available. However,

489   water limitation will occur increasingly, particularly in the Mediterranean region during summer.

490   Water limitation of forage production can to some extent be alleviated by higher CO_2

491   concentration, which increases the water use efficiency, and by a shift in productivity towards

492   the cooler part of the year in Mediterranean climates. The effect of climate change on plant

493   winter survival in the Nordic region is difficult to predict due to interactions between

494   temperature and snow cover on winter stress levels, and the interactions between temperature

495   and light factors on cold acclimation and deacclimation processes. Other uncertainties regarding

496   increased forage production in the Nordic region in the future climate includes water saturated

497   soils and soil compaction, practical problems with cultivation and harvesting, and increasing

498   occurrence of weeds, pests and diseases. Climate change can affect forage quality in several

499 ways in both Nordic and Mediterranean regions through its effects on plant growth and

500 development as well as species composition.

501 In the face of unstable and uncertain climatic conditions, a high diversity of cultivated forage

502 species, high intraspecific genetic diversity, and the use of species and variety mixtures can

503 enhance productivity and resilience of grasslands. In both the Mediterranean and Nordic regions,

504 climate change will lead to changes in the annual growth patterns of grassland species (both

505 growth rates and timing of growth), prompting adaptations of fertilization and defoliation

506 regimes (timing and intensity). Breeding and research efforts should be stimulated towards (i)

507 improving plant strategies to cope with relevant stresses in appropriate ways (e.g. maintenance of

508 growth under moderate stress and survival under severe stress), (ii) optimizing the regulation of

509 growth so that it fits new seasonal climate and defoliation patterns (e.g. increase growth potential

510 during the cooler part of the year in the Mediterranean region or during spring in the Nordic

511 region, and improve regrowth capacity after defoliation in the Nordic region), and (iii) utilizing

512 plant diversity at all levels (e.g. develop mixtures with inter- and intraspecific variation in

513 responses to climatic variables).

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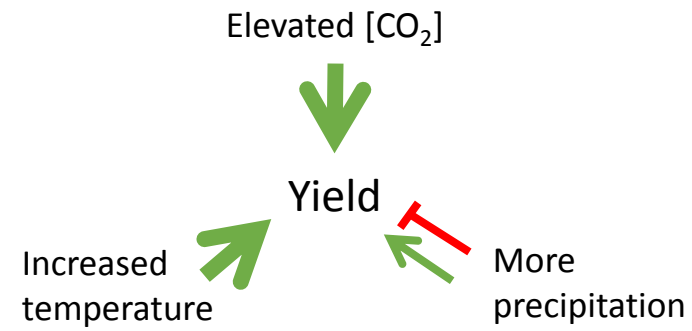
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915   Figure legend

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

930

(A) Nordic

Elevated [CO_2]
Yield
Increased temperature
More precipitation

(B) Mediterranean dry/hot

Elevated [CO_2]
Yield
Increased temperature
Less precipitation
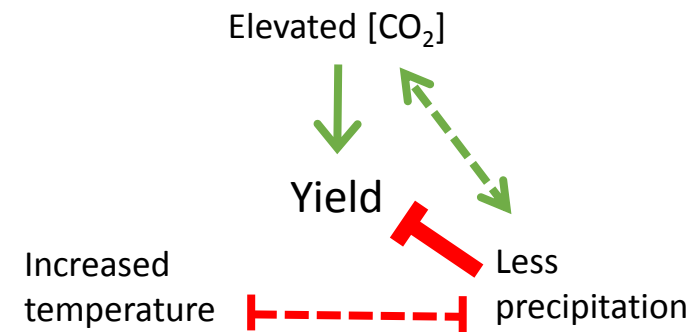
(C) Mediterranean less dry/less hot

Elevated [CO_2]
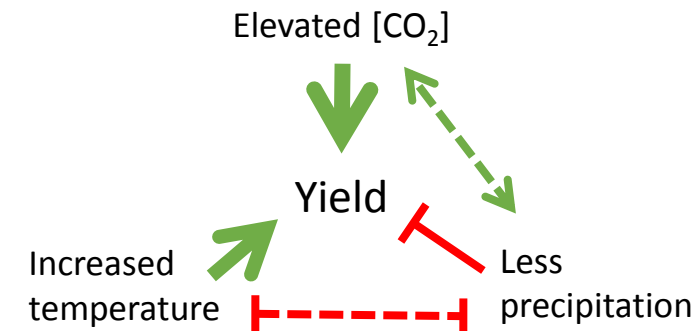Yield
Increased temperature
Less precipitation

Table

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

		Nordic	**Mediterranean**
Growing season	**Current timing**	April - early June to Mid-September - early November[1]	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 [*, 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**	Mid-September - early November to April - early June[1]	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] **3)** 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]

[*]change associated with high uncertainty

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], 2017[11], Ruosteenoja *et al.,* 2007[12], Kellomäki *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.,* 2014[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]