Isabel Roldán-Ruiz
Joost Baert
Dirk Reheul *Editors*

Breeding in a World of Scarcity

Proceedings of the 2015 Meeting of the Section "Forage Crops and Amenity Grasses" of Eucarpia

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Preface

The 31st Eucarpia Fodder Crops and Amenity Grasses Congress took place in Ghent, Belgium, on 13–17 September 2015. Attendance was good, with 124 scientists and breeders from 25 countries. The Institute for Agricultural and Fisheries Research (ILVO) and Ghent University were co-organizers; it was the third time that Belgium had the honor of hosting this congress.

The theme of the meeting was "breeding in a world of scarcity." Scientific presentations and discussions were divided into four sessions: (1) scarcity of natural resources, (2) scarcity of breeders, (3) scarcity of land, and (4) scarcity of focus. Session 1 refers to the consequences of climate change, reduced access to natural resources, and increased pressure for adopting more sustainable agricultural practices. Global warming results in more extreme weather conditions. Biodiversity and genetic resources are under pressure as a consequence of climatic change and anthropogenic actions. High-yielding crops require high doses of nutrients with shrinking availabilities. Plant breeding may help by developing varieties with a more efficient use of water and nutrients and a better tolerance to biotic and abiotic stress. Session 2 refers to the shrinking number of breeders. Field breeders are becoming a rare breed, and modern plant breeders are expected to combine knowledge from different disciplines far more than in the past. There is a need for a mutual empathy between field-oriented and lab-oriented breeding activities. New methods of phenotyping and genotyping need to be integrated in breeding and bridge the gap between lab and field. Session 3 deals with the scarcity of agricultural land. Agricultural land has to be optimally used. Forage needs to be intensively produced in a sustainable way, at a competitive cost while still meeting the energy, protein, and health requirements of livestock. Well-adapted varieties, species, and mixtures of grasses and legumes are needed, not only to use as feed but also to use as turf and bioenergy and to provide ecosystem services. Session 4 refers to the fading of focus in primary production triggered by a range of societal demands. There are few farmers left, and they are asked to meet many consumer demands. Various crops and management systems are involved. Both large-scale, multi-purpose species and varieties and specialized niche crops are required to fulfill all these diverse needs and expectations.

This book contains the invited and submitted papers presented at the conference, whose Parts I, II, III, and IV correspond to the four sessions described above. Part V summarizes the conclusions of the debates, working groups, and workshops held during the meeting. Two open debates were organized: one on the future of grass and fodder crop breeding and a second one on feed quality breeding and testing. The content of these debates was determined on the basis of a survey in which several breeding companies and institutes participated. Different, and sometimes contrasting, views of these topics were presented and discussed in plenary sessions. The 31st section conference hosted meetings of two working groups, namely, "Multisite rust evaluation" and "Festulolium." During the "genomic selection and association mapping" workshop, participants shared experiences about the use of genetic and genomics tools in forage crop breeding. In the "phenotyping" workshop, current applications of noninvasive phenotyping tools in forage crop breeding research were presented, with a focus on the implementation in practical breeding. Part V contains also short sketches of breeding ideas presented as short communications by conference participants meant to help create progress in forage crop breeding.

We gratefully acknowledge the efforts of the members of the scientific committee (Ulf Feuerstein, Roland Kölliker, Paolo Annicchiarico, Philippe Barre, Susanne Barth, Johan De Boever, Alex De Vliegher, Trevor Gilliland, Mike Humphreys, Bernhard Ingwersen, Bernadette Julier, Petter Marum, Jan Nedelnik, Ulrich Posselt, Niels Roulund, Daniele Rosellini, Dejan Sokolovic, Leif Skot), for the critical review of the offered papers. Their pivotal contribution ensured the high quality of the chapters included in this book. Special thanks go to Miriam Levenson (ILVO) for the careful English-language editing of all submissions.

The local organizing committee (Jonas Aper, Mathias Cougnon, Johan De Boever, Alex De Vliegher, An Ghesquiere, Geert Lejeune, Katrien Liebaut, Nancy Mergan, Hilde Muylle, Tom Ruttink, Ariane Staelens Kristiaan Van Laecke, and Tim Vleugels) did a great job before, during, and after the meeting. It was a pleasure to organize the conference with such a good, tight team.

Finally, we express our gratitude to all the participants for daring to attend a meeting peppered with unconventional formats and for their valuable contributions to the presentations, debates, and discussions.

Melle and Ghent, Belgium

Isabel Roldán-Ruiz
Dirk Reheul
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Part I

Scarcity of Natural Resources

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Breeding Forages to Cope with Environmental Challenges in the Light of Climate Change and Resource Limitations

Á. Helgadóttir, L. Østrem, R.P. Collins,
M. Humphreys, A. Marshall, B. Julier, F. Gastal,
Ph. Barre, and G. Louarn

Abstract

Global climate change and increased pressure for adopting more sustainable agricultural practices call for new approaches in breeding forage crops. In the cool temperate regions of Europe these crops may benefit from a warmer and prolonged growing season, but new stresses may emerge during autumn and winter, whereas further south risk of drought will increase. In addition, future forage crops have to use both nutrients and water more efficiently maximize production per unit area. This paper presents examples of how perennial forage crops can be adapted to the projected European environmental conditions through breeding. In the Nordic region, the focus is on identifying traits that are important for high yields under changed overwintering conditions and management practices. In temperate maritime Europe, the breeding focus is on forage grass and legume root systems for ecosystem service, nutrient and water use, as well as the advantages and potential for Festulolium, including its role in ruminant nutrition. In temperate and southern Europe, breeders aim to develop varieties that can survive long drought periods and recover rapidly following autumn rains, as well as improving adapted legume species with the following aims: reducing use of synthetic fertilizers, mitigating the environmental impacts of ruminant production systems; and reducing

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their dependency on external protein-rich feeds. Forage production systems, which are commonly found in areas less suited to grain production, can contribute significantly to future food security but only if forage crops can be successfully adapted to meet future environmental challenges.

Keywords
Breeding • Climate change • Environmental sustainability • Forage crops

Introduction

The rising world population and a rapidly growing middle class are projected to result in increased demand for high quality food products from ruminants, both meat and milk. This demand is projected to nearly double by 2050 (FAO 2006). The corresponding increases in emissions of biogenic greenhouse gases (GHG) are expected to be the main driver for the projected temperature increase towards the end of this century (IPCC 2013). Agriculture is responsible for around one-third of global GHG emissions, of which 37 % of the methane production comes from livestock (FAO *loc. sit.*). Agrochemicals have polluted waterways, biodiversity is being threatened by intensive cultivation, and groundwater use is unsustainable in many places. Strategies must be found to meet the expected demand for animal products without further compromising the environment (Tilman et al. 2011). Ruminant products can be obtained from either grain or pasture-based systems. Grain-based feed competes directly with food for people, whereas pasture systems convert plant material unsuitable for human consumption into valuable food products. Such systems are commonly found in areas that are less suitable for grain production; they are dominated by grasslands and forage crop production. They can therefore contribute significantly to human food security by adding both calories and protein (Foley et al. 2011).

Changing climatic conditions and the increased pressure for adopting more sustainable agricultural practices will alter the suitability and profitability of the pasture systems currently employed in different parts of the world. In the cool temperate regions of northern Europe, global warming is expected to increase productivity primarily because of an extended growing season and longer frost-free periods (Olesen et al. 2011). At the same time, new stresses may emerge, especially in relation to overwintering of perennial species (Höglind et al. 2013). In large parts of southern Europe, conditions for summer crop production are expected to deteriorate, primarily due to increased risk of drought, whereas the growth period will be extended in late autumn and early spring (Olesen et al., *loc. sit.*). In all European regions, forage crops will have to use both nutrients and water more efficiently to maximize production per unit area. The use of N-fixing species should be emphasized to reduce the energy required to produce artificial fertilizers and to improve the protein autonomy of animal fodder in Europe. In addition, forage production systems will need to contribute to additional ecosystem services (soil, air and water quality, reduction of GHG from agriculture, and biodiversity conservation). Various options are available for adapting pasture systems to a changing climate and limited resources, from modifying or making substantial changes to current production systems to developing completely new systems (Lee et al. 2013). Breeding of forage crops has an important role to play in this evolution. One route is to develop new varieties of currently-grown species by identifying traits that improve their ability to cope with the expected environmental challenges. Exotic material can also be introduced and adapted to a new environment. Selecting the best approach will require information on various factors, such as the potential impact of climate change on the environment in question, the available genetic variation within gene pools of the relevant species, and the potential for introducing exotic material into existing breeding programs without sacrificing already-obtained improvements. Desired traits will be improved forage quality, increased resistance to biotic and abiotic factors, fine-tuned plant development processes and maximized resource use efficiency (Kingston-Smith et al. 2013).

This paper gives examples of how perennial forage crops can be adapted to the projected environmental conditions in three main European climates: Nordic, temperate maritime, and temperate or Mediterranean.

The Nordic Environment

Environmental Conditions and Projected Future Climate

The Nordic region of Europe (55–70 °N) has mild sea currents that result in average temperatures several degrees higher than comparable latitudes anywhere in the world. Within the region climatic conditions can vary considerably. The main limiting factors for forage crops are a short and moderately cool growing season and various winter stresses such as frost, ice encasement, low temperature fungi, prolonged snow cover, water logging and low light intensity. A rise in average temperature is projected to be similar to the global mean in the south and west part of the region (2.6–4.8 °C), and nearly double that in the north and east (Nordic Council of Ministers 2014). The highest increases will be seen during winter and in areas with a continental climate. Precipitation is predicted to increase in most parts of the region, especially in winter, but summer precipitation may be more evenly distributed and may even decrease in the southernmost part of the region (<60 °N). More extreme precipitation events are expected. The expected changes in climate at northern latitudes will result in a longer growing season with higher temperatures during the growing season, and increased biomass production potential. A modeling approach based on currently-grown timothy (*Phleum pratense* L.) cultivars across Norway demonstrated that increased biomass production was primarily attributed to more cuts per growing season (Persson and Höglind 2014). However, disease pressure and complex interactions between various environmental factors influencing overwintering may offset the potential gain (Rapacz et al. 2014). In continental sites with reduced snow cover, frost injury during winter for timothy may increase while more extensive damage is expected for the less adaptive perennial ryegrass (*Lolium perenne* L.) (Thorsen and Höglind 2010).

Adaptive Strategies in Response to Climate Change

The interaction of temperature and photoperiod controls the local adaptation of perennial forage crops by governing important physiological processes such as vernalization, flowering and cold acclimation. This interaction in turn determines winter survival and seasonal yield distribution. The projected climatic changes will lead to increased temperatures while seasonal photoperiod remains unchanged. Plants need to be adapted to different combinations of climatic variables and possess higher biomass production potential. We should therefore consider factors such as growth cessation in autumn in relation to acclimation, deacclimation and reacclimation, carbohydrate dynamics during autumn and winter, and photosynthetic activity and respiration at low temperature and light intensity.

For the foreseeable future, timothy is likely to remain the most common forage grass species grown in cold temperate regions at higher latitudes (Østrem et al. 2013). With a prolonged growing season, worthy breeding goals would be to improve its regrowth capacity and to make better use of favorable conditions in spring/early summer for elongation growth and production, while simultaneously avoiding the risk of frost damage in late winter (Rapacz et al. 2014). Perennial ryegrass and Festulolium (×*Festulolium* Aschers. et Graebn.) are currently grown in maritime regions but cannot be reliably grown inland and north of 60 °N. These high yielding species with good regrowth capacity and superior feed quality will become a promising option for a prolonged growing season and milder winters. Studies of their growth cessation and photosynthetic acclimation have shown a clear relationship between leaf elongation rate and photosynthetic acclimation, thus implying an inadequate autumnal growth cessation for sufficient cold acclimation (Østrem et al. 2014). Significant G×E interactions for biomass production, regrowth capacity and winter survival in recent cultivar trials reflect the considerable variation in climatic conditions in the Nordic region (Østrem et al. 2015), showing the importance of regional testing to find the optimal cultivars for persistence and production at each location.

The onset of acclimation is expected to start later in the autumn at lower solar radiation levels and thus less optimal conditions. Studies in controlled environments have shown reduced cold acclimation efficiency for northern varieties of perennial ryegrass and timothy compared with more southern ones when the temperature is higher than normal during preacclimation (Dalmannsdóttir et al. 2015). An increased use of non-native species in future conditions will therefore depend on plants being adapted to unique combinations of photoperiod and temperature during autumn. A sensible strategy for future breeding programs should be to select genotypes where growth cessation is controlled by photoperiod rather than temperature, while still maintaining a certain level of photosynthetic activity in autumn in order to build up sufficient carbohydrate reserves for winter survival (Østrem et al. 2014). At warmer winter temperatures, warm spells in mid-winter may trigger deacclimation and cause premature elongation growth. In perennial ryegrass it will probably be more efficient to increase the maximum frost tolerance rather than improve the ability to reacclimate after warm spells during unstable winters (Nordic Council of Ministers 2014). Additionally, waterlogged soil in autumn is expected due to increased precipitation (IPCC 2013). Freezing tests have indicated that increased abiotic stress caused by higher levels of waterlogged soil may enhance frost tolerance of timothy and red clover at low temperatures. At higher temperatures, hardening of red clover was reduced because of higher respiration and reduced assimilation rates, whereas timothy was less affected (Dalmannsdóttir et al. 2012).

The current genetic diversity in perennial ryegrass, timothy and meadow fescue (*Festuca pratensis* Huds.) found in the Nordic region is rather restricted, as it probably originates from a limited number of introductions (Rognli et al. 2013). Future breeding, irrespective of crop species, requires efficient ways to incorporate wild adapted genetic resources and exotic material into the current breeding base. This long-term task requires public support and active knowledge transfer from public-sector scientists into real-life crop improvement (Helgadóttir 2014). A good example is the Nordic Public-Private Partnership (Nordgen 2015) on pre-breeding of perennial ryegrass. Approximately 400 diverse accessions have been phenotyped, recombined to introgress exotic germplasms, and genotyped by sequencing to estimate relatedness and develop tools for associating genome regions with traits. These efforts will result in locally adapted germplasm for specific climates/sites and germplasm with wide adaptations (phenotypically stable) (Nordic Council of Ministers 2014).

Forage legumes play a vital role in future sustainable agriculture, and in the Nordic region both red (*Trifolium pratense* L.) and white clover (*T. repens* L.) cultivars are sold. In white clover, adequate genetic variation for cold tolerance and rapid adaptational changes have been manifested (Helgadóttir et al. 2001). Generally, persistent types are small-leaved with low production potential but simultaneous selection for yield and winter hardiness has been successful following hybridization between northern and southern adapted populations (Helgadóttir et al. 2008). Red clover shows extensive variation for yield but the basis for genetic variation of cold tolerance has been less investigated than in white clover (Annicchiarico et al. 2015). A recent study using molecular markers has demonstrated rapid genetic change of diverse populations when grown in contrasting environments (Collins et al. 2012). When developing red clover cultivars for the current and future climate in the north, similar to perennial ryegrass, it is important to broaden the genetic base and identify valuable material for future pre-breeding and breeding projects. One such project is currently being undertaken where wild material and landraces in the Nordic collection of red clover are evaluated at four locations across the Nordic region.

Temperate Maritime Environments

The UK climate is predicted to include warmer, wetter winters and hotter, drier summers with increasing frequency of extreme weather events (Harrison et al. 2001). Incidents of soil waterlogging, floods, or droughts will all have significant effects when occurring separately, and when they occur in sequence, ever-increasing incremental effects are expected that will reduce grassland production and crop persistence in the UK. Soil hardening after summer droughts will result in heavily compacted soils, which in turn will exacerbate the effects of high rainfall events in autumn. We propose that improvements in plant traits affecting waterlogging and drought tolerance can be delivered through breeding for combined deeper and more extensive root systems of major grassland species, and will pave the way for improved, agronomically superior forage varieties that also deliver environmental services including improved soil hydrology and carbon sequestration.

In European temperate maritime environments, the need for grassland swards that produce above-ground biomass of sufficient quality to sustain high levels of animal performance while also delivering ecosystem services is well-recognized (e.g., Isselstein and Kayser 2014). In temperate forage species, breeding for above-ground sustainability traits such as stress resistance and forage quality has made rapid progress (Abberton et al. 2008) but the design of root systems has received considerably less attention. The technical difficulties associated with investigating the functioning of plant root systems *in situ* have diminished full appreciation of their potential to deliver multiple environmental benefits. However, with the development of improved phenotyping technologies and increased emphasis on sustainable grassland systems, the links between root system traits and environmental functioning (Bardgett et al. 2014) are now a major research focus.

Plant roots have a greater impact on soil water status than different capacities for water extraction alone (Macleod et al. 2007). Hydrologists have described a pivotal role for vegetation in the regulation of soil water content, including root activity that can initiate biophysical changes in soil hydraulic properties (Whalley et al. 2005), that occur in function of the porosity of the soil and the rooting depth of the vegetation. Developments in dynamic root imaging, combined with an increased understanding of the genetic base of variation in root architecture, could bring about a step change in our awareness of how forage plant root systems may be designed to balance above-ground biomass productivity and below-ground biotic and abiotic interactions. Plant breeding approaches at IBERS (Wales, UK) now involve novel phenotyping systems that can be used at different scales (from genotype to farm system) to enable quantification of the impact of plant root systems on important aspects of soil quality. As proof of principle, rainfall run-off was measured over a 2-year period using hydrologically-isolated field plots, each containing varieties of different *Lolium* and *Festuca* species. The Festulolium variety, cv. Prior (a hybrid of *L. perenne* and *F. pratensis*), had a 51 % lower run-off than a current *L. perenne* variety and 43 % lower than *F. pratensis*. In a detailed phenotyping study, cv. Prior produced very large root systems which subsequently degenerated extensively, especially at depth, leading to significantly enhanced soil porosity. This trait assisted soil water retention and reduced over-land flow compared to its parent species and the other grasses assessed (Macleod et al. 2013). The outcome of these observations led to a 5-year project, SUREROOT (http://www.sureroot.uk/), that includes use of two UK National Capability Facilities, the National Plant Phenotyping Centre (NPPC) at IBERS (Aberystwyth) and the Farm Platform at North Wyke (Devon). Detailed analyses of root ontogeny involving both grasses and clovers are being obtained in the NPPC and changes measured over time. The impacts of root architecture and ontogeny on soil structure and hydrology under different field conditions and livestock management systems is being compared to assess the potential for a combined strategy for grassland that provides high agronomic value and flood mitigation.

Exploiting interspecific and intergeneric hybrids in forage grasses and legumes

1. Festulolium: The research carried out in SUREROOT uses novel Festulolium hybrids that include the attributes of both *Lolium* and *Festuca* species, but may also outperform their parent species in a number of growth and performance traits. Predicted climate change scenarios open the possibility for including novel grasses previously considered suitable for livestock production systems in temperate maritime environments (Kingston-Smith et al. 2013). Examples include hybrids involving either *L. multiflorum* or *L. perenne* together with *F. arundinacea var glaucescens,* a drought and heat-tolerant grass species found in Mediterranean regions. This has potential to restrict plant mediated proteolysis in the rumen, and reduce greenhouse gas emissions and N losses by livestock (O'Donovan 2015). This germplasm is also deep rooting, which has enhanced its drought resistance (Durand et al. 2007), consistent with alternative hybrids involving *Lolium* spp. and *F. mairei* (Atlas fescue). All of this germplasm has high forage yields and excellent nutritive value (Humphreys et al. 2014) and will be employed in the SUREROOT project in addition to two diploid drought-tolerant introgression-lines formed following transfers of genes for drought resistance from chromosome three of two *Festuca* species into *Lolium* (Humphreys et al. 2012). Natural Festulolium hybrid combinations also exist and contain potentially useful adaptations for use in plant breeding such as novel genetic variants for flooding tolerance. For example, *Festulolium loliaceum* (derived from hybridization of *L. perenne* and *F. pratensis*) is found in flood- and water-meadows, and appears better adapted to waterlogging than either of its parental species (Humphreys and Harper 2008).
2. *Trifolium repens* × *T. ambiguum* hybrids: Wide genetic variation within the gene pool of white clover has been used successfully in the production of new varieties with improvements in many traits. However, less variation has been identified for traits such as drought tolerance, which is difficult to improve significantly by conventional selection (Abberton and Marshall 2005). Caucasian or Kura Clover (*Trifolium ambiguum* M. Bieb.) is a rhizomatous perennial legume species with good drought tolerance and persistence (Coolbear et al. 1994). Hybrids have been developed between white clover and Caucasian clover (Marshall et al. 2001) to introgress the rhizomatous trait from the latter as a strategy for improving drought tolerance while retaining the desirable agronomic traits associated with white clover. Fertile backcross (BC) hybrids (derived from backcrossing to white clover) have been produced that are essentially like white clover, but which have rhizomes and stolons. A drought experiment carried out in deep soil bins showed that the hybrids maintained lower values of leaf relative water content (RWC) and leaf water potential than Caucasian clover, but higher levels than white clover at the same level of drought. The mechanism by which Caucasian clover maintains a higher leaf RWC is not known, but it has been established that this species and both generations of the BC hybrids allocate a higher proportion of their total DM yield to roots than white clover, *i.e.,* they maintain a higher root weight ratio (Marshall et al., *loc. sit.*). A recent experiment (Marshall et al. 2015) compared the below-ground morphology of plants of Caucasian clover, white clover, and the BC hybrids grown in 1 m long plastic 'root pipes' (Fig. 1.1). Caucasian clover had a greater root weight than white clover at depths below 0.2 m. The BC1 and BC2 hybrids also had a greater root weight than white clover at depths below 0.2 m, which suggests that introgression increased the allocation of resources to roots at lower depths, thereby contributing to the improved drought tolerance of the BC hybrids compared with white clover. This is

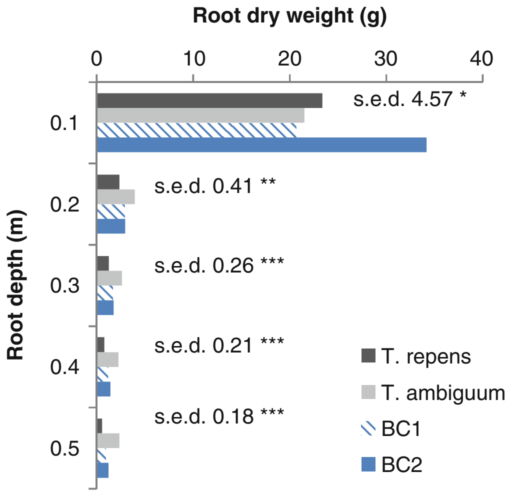

Fig. 1.1 Root dry weight in 0.1 m sections of soil columns containing *T. repens*, *T. ambiguum*, BC1 and BC2 hybrids

likely to be advantageous in environments where water reserves exist at depth. Conversely, where moisture reserves are confined to the upper layers of soil, then root depth becomes less important than the ability of plants to produce an efficient extraction system in these surface layers. Although the depth of root systems depends on soil type, cultivar and management, white clover is generally considered to be a shallow-rooted species, with most roots distributed in the top 0.1–0.2 m of soil (Caradus 1990). This distribution pattern is likely to reduce the ability of the species to persist under drought, and suggests a mechanism through which the BC hybrids, with greater root weight than white clover below 0.2 m, are more drought tolerant than their parent.

The Southern European Environment

Environmental Conditions and Projected Future Climate

Southern Europe is characterized either by a temperate climate or (along the Mediterranean Sea) a Mediterranean climate. The average annual temperature of southern Europe is expected to increase: more during summer (3–4 °C across the Iberian Peninsula) than during winter (1.5–2 °C) (IPCC 2013). More frequent hot summers and fewer cold winters are therefore expected to occur. Annual rainfall is expected to decrease between 0 and 10 % in southern areas, particularly during the summer (IPCC 2013). As evapotranspiration is also expected to increase due to the rise in temperature and solar radiation, soil water deficit should increase more than the projected decrease in summer rainfall. This trend is exacerbated by the extremely limited potential for irrigation. Crop simulation models show that rises in CO_2 concentration and in autumn-winter-spring temperatures are both favorable to forage production but would not compensate for the decrease in summer production (Durand et al. 2010). To cope with these new constraints, several key actions could be considered. First, new varieties can be created which are better adapted to new climatic conditions. Second, forage legumes in forage production systems can be increased. Legume species can be used in pure or mixed swards. They can also be used in rotations to accomplish three aims: (1) reduce the use of mineral N fertilizers, (2) reduce environmental impacts of ruminant systems (nitrate leaching, N_2O and methane emissions) (Lüscher et al. 2014) and (3) to increase the persistency of perennial grasslands to support severe drought periods, favor carbon storage and biodiversity and avoid soil erosion. Forage for the driest areas can be based on self-reseeding winter annuals.

Strategies to Adapt Forage Species to Climate Change in Southern Europe

In southern Europe, lucerne (*Medicago sativa* L.), tall fescue (*Festuca arundinacia* Schreb.) and cocksfoot (*Dactylis glomerata* L.) are the most cultivated perennial species. Interest in these species is reinforced by the expected impacts of climate change. The large diversity of ecotypes, landraces and varieties adapted to various Mediterranean conditions have been little used in breeding programs thus far (Lelièvre and Volaire

2009; Annicchiarico et al. 2013; Poirier et al. 2012). A few annual species are also used as annually self-regenerating pasture (e.g., subterranean clover, annual medics, annual ryegrass) in Mediterranean areas (Grashaw et al. 1989; Texeira et al. 2014). These forage species rely on seed production and survival in the seed bank to avoid summer droughts and may become more important to overcome prolonged periods of stress in the driest areas.

Lucerne, a major legume species traditionally cultivated in many areas of southern (and eastern) Europe, has a high potential for biomass and protein production. It is well suited to provide ecosystem services in forage-crop rotations, because it can supply large amounts of N to subsequent crops, improve soil structure and capture nitrate in soils. Considering climate change, the choice of the best adapted lucerne varieties should focus on the autumn dormancy range. This dormancy, driven by both low temperature and short photoperiod, induces a reduction of vegetative growth that is related to winter survival. With mild temperatures in autumn and spring and less severe frost in winter, dormancy could skip from 4–5 (Flemish types) to 5–6 (known as Mediterranean types in France) in temperate Europe and from 5–6 to 7–8 in Mediterranean Europe, on a dormancy scale ranging from 1 (winter-dormant) to 11 (winter-active). The varieties of temperate and Mediterranean origin have a similar developmental response to temperature but the Mediterranean cultivars have a lower productivity potential and photosynthesis at high temperatures (G. Louarn, pers. comm.). Part of the breeding effort currently devoted to Flemish types should now be transferred to Mediterranean types by using classical breeding criteria (forage yield, disease and pest resistance, feeding value, lodging resistance, seed production). For Mediterranean climatic conditions in the context of climate change, development of lucerne varieties adapted to rain-fed conditions is an objective (http://reforma.entecra.it/). Landraces traditionally grown in rain-fed conditions have shown interesting agronomic performance in a multi-site trial in northern and southern Mediterranean regions (Annicchiarico et al. 2011a). Combining adapted autumn dormancy and tolerance to summer drought would create lucerne varieties tolerant to Mediterranean climates in a water-restricted sustainable agriculture.

Mixtures of lucerne and perennial grasses can be used to meet the requirement of an energy and input-limited agriculture. Mixtures grown with no or little N fertilization or herbicides have to produce at least as much forage as the best yielding species grown in pure stand and/or to improve annual yield distribution, and the forage must have a well-balanced N/energy ratio. Usually varieties are bred for pure stand performance, considering that a good variety in pure stand is also good in mixture. However, in recent experiments, we have found that forage production and quality of lucerne varieties in mixture was only partly related to their performance in pure stands (Julier et al. 2014).

To cope with dry conditions, perennial grasses have developed different strategies either to produce (drought resistance) or survive (drought survival) during drought (Volaire et al. 2009, 2014). For forage species, drought resistance is targeted in areas subjected to moderate droughts, while drought survival is the main objective for areas with severe and chronic droughts. To achieve drought resistance or survival, the main physiological mechanisms are classified as dehydration delay (or avoidance) of either lamina or meristems, dehydration tolerance of either lamina or meristems and summer dormancy (Volaire et al. 2009). However, there is a general trade-off between summer dormancy and productivity under favorable conditions of autumn and spring (Shaimi et al. 2009). An ideotype has been defined that would be highly drought tolerant through summer dormancy but nevertheless productive at other seasons.

There is a gradient of winter "dormancy" (i.e., reduction of plant growth) with latitude from Mediterranean ecotypes to Nordic ecotypes. Mediterranean ecotypes grow continuously from autumn to spring when water is not a limiting factor. In contrast, Nordic ecotypes have a long growth cessation from autumn to spring that confers cold tolerance, but they are characterized by a vigorous spring-summer growth (Annicchiarico et al. 2011b; 2013). New plant material could be created with high leaf growth rates (related to forage productivity) and different levels of summer and winter dormancy, depending on the climatic region targeted. It is possible to select for productivity in Mediterranean material or to gather favorable traits from Mediterranean material (dehydration tolerance, growth during mild and humid seasons, i.e. autumn, winter, spring) and from elite temperate material (forage productivity, cold and disease resistances and seed productivity) (Barre et al. 2014).

The use of self-regenerating annual species has been reported to increase forage production, soil fertility and carbon sequestration, and they are more resilient than perennials to extreme climatic events (Wolfe and Dear 2001; Texeira et al. 2014). The adaptability of self-regenerating annual species is governed by traits enabling them to complete seed production over the duration of the local growing season (determined by winter rainfall and summer drought). The flowering and maturity dates are critical. The ability to overcome low or zero seed production during extremely stressful years or management has been obtained by selecting varieties with hard-seededness, ensuring persistence in the seed bank and long-term regeneration (Reed et al. 1989).

Adaptation of grass and legume species could also be obtained by mixing Mediterranean and temperate types into mono- or pluri-specific mixtures. Mixing such types of tall fescue, cocksfoot and lucerne in monospecific mixtures may help to regulate forage production during the year and to reduce the disequilibrium between spring and summer production (http://www.animalchange.eu/). This approach was particularly interesting in the case of grass-lucerne associations, with both seasonal growth complementarities between the species and the plant types, and positive N facilitation effects brought by the legume to the grass species. In another design, in which both the number of species and genotypes varied, multispecies mixtures were more productive than monocultures in dry conditions but it was shown that the temporal stability of production increased with the number of genotypes only (Prieto et al. 2015). Use of species and population diversity could be beneficial to forage productivity in constrained environments but requires adapted cultivars that can resist drought, cold and N-limited conditions.

Conclusion

Forage production systems, commonly found in marginal areas less suited to grain production, can contribute significantly to future food security – but only if forage crops can be successfully adapted to future environmental challenges.

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2

Performance of Diploid and Tetraploid Perennial Ryegrass Synthetics with Variable Numbers of Parents

B. Boller, C. Grieder, and F.X. Schubiger

Abstract

When building synthetic varieties by crossing a fixed number of elite genotypes in a polycross, breeders are faced with a tradeoff between selection intensity and inbreeding depression. We investigated the relationship between synthetic size and herbage dry matter (DM) yield by analyzing replicated field data of 93 diploid and 73 tetraploid perennial ryegrass (*Lolium perenne* L.) synthetics of the Agroscope breeding program. In line with theoretical expectations, DM yield of diploid synthetics declined when the number of parents dropped below seven. However, no such decline was observed with tetraploid synthetics. We conclude that in tetraploid perennial ryegrass, selection intensity can be increased to result in synthetics with only five parents without hampering DM yield.

Keywords

Parent number • *Lolium perenne* • Polycross • Synthetic • Breeding • Dry matter yield

Introduction

Synthetics built by cloning and polycrossing a fixed number of elite parent genotypes are the most common type of cultivar in forage grass breeding. When selecting the parental elite genotypes of a candidate cultivar, breeders must consider the tradeoff between selection intensity and inbreeding depression occurring during seed increase of the synthetic. This decrease in performance of the syn-2 and following generations, caused by mating of related individuals, will be the more pronounced the fewer parents form the initial polycross. The theoretical foundation of this relationship, mathematically captured by the so-called Sewall Wright formula, was comprehensively described by Posselt (2010) for the case of perennial ryegrass (*Lolium perenne* L.). He modeled performance of synthetics based on experimental

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data of diploid perennial ryegrass and found that the optimum number of parents for maximum yield was between 7 and 11. Recently, attempts were made to reduce the effect of inbreeding in few-parent-synthetics by choosing, with the aid of molecular markers, genetically more distant genotypes (Kölliker et al. 2005). Ghesquiere and Baert (2007) and Baert et al. (2007), in model experiments, investigated the possibility of narrowing a perennial ryegrass synthetic down to as little as two parents. They concluded that inbreeding depression was less important in tetraploid than in diploid material, and less important for herbage than for seed yield. In this study, we test (i) if the size-performance-relation as observed in practical breeding follows theoretical expectations and (ii) if there is a difference in optimum synthetic size between diploid and tetraploid plants. The results suggest that when using tetraploid breeding material of perennial ryegrass, the risk of a decrease in performance with too-few constituents of a synthetic is minimal.

Materials and Methods

Plant Material and Experimental Data

The study is based on results obtained in Agroscope's perennial ryegrass breeding program. Data encompass a total of 93 diploid and 73 tetraploid synthetics, created between 1987 and 2009 and composed of 5–68 parents. Out of these, 7 diploid and 12 tetraploid synthetics reached the status of a cultivar listed in at least one country.

In Agroscope's breeding scheme (see Humphreys et al. 2010), after cloning and polycrossing a number of genotypes (Ng), the progeny of each genotype is sown in replicated rows and a selected number of half-sib progenies (Np) is allowed to inter-pollinate and set seed. Bulk seed harvested on these progenies constitutes the synthetic. We describe the size of the synthetic as Np + (Ng − Np)/2, considering that Np genotypes deliver their full and (Ng − Np) half their genetic makeup into the synthetic. All synthetics of this study were tested in field trials, carried out between 2000 and 2014 at Zürich-Reckenholz (47.43°N, 8.52°E), Ellighausen (47.61°N, 9.14°E) and Oensingen (47.28°N, 7.73°E), Switzerland. Field trials consisted of 1.5 × 6 m plots with three replications arranged in Latin rectangles and were harvested five times in both the first (H1) and second (H2) main harvest year. Total dry matter (DM) yield was determined by weighing fresh herbage with a plot harvester followed by DM determination via oven drying. Most entries were sown in at least 2 years at all three locations, resulting in yield data from six "environments" (combination of location and year of sowing). However, deviations were possible with some entries being sown in only one or in more than 2 years (especially those reaching status as a standard cultivar). On average, each entry was tested in 6 (2–32) environments.

Statistical Analysis

In a first step, least squares means of total DM yield of H1 and H2 were estimated for each synthetic using general linear models. Combined analysis over all series of trials was possible through overlapping entries between trial series, even though there was no common set of standard varieties in all trials. The following statistical model was used:

$$y_{ijn} = \mu + s_i + e_j + r_{jn} + \varepsilon_{ijn} \qquad (2.1)$$

where μ is the general mean, s_i is the effect of the ith synthetic, e_j the jth environment, r_{jn} the nth replication within the jth environment and ε_{ijn} the residual. Mean performance of each synthetic was then regressed on the two covariates "year of polycross creation" (p) and "time of inflorescence emergence" (f) to correct for the general breeding progress achieved over the years or any effect of earliness, respectively:

$$y_i = \mu + xp_i + yf_i + \varepsilon_i \qquad (2.2)$$

Finally, the residuals (εi) from Eq. (2.2), i.e. the deviation from the predicted yield of synthetic i, were regressed on synthetic size to evaluate the size-performance-relation. Since tetraploid synthetics clearly outyielded diploid ones irrespective of synthetic size, separate regression analyses were performed for these two groups. SAS® procedures were used for all statistical analyses.

Results and Discussion

DM yield of tetraploid synthetics exceeded that of diploids by 8.5 % in H1 and by 12.9 % in H2 (Table 2.1). Overall, early synthetics yielded significantly higher in H1 but the influence of earliness in H2 was not significant. General breeding progress was rather slow but significant for both H1 and H2. These differences justify considering ploidy, earliness and year of polycross in the subsequent analysis of the influence of synthetic size on performance.

Diploid and tetraploid synthetics differed in the relationship between synthetic size and yield in H1 (Fig. 2.1). A significant decline of DM yield with lower number of parents was observed in the diploid, but not in the tetraploid synthetics. The decline of yield with lower numbers of parents in the diploid synthetics was best described by a highly significant ($p = 0.0006$) hyperbolic regression (Table 2.2).

Table 2.1 Influence of ploidy level, earliness and year of polycross on herbage dry matter yield of 166 perennial ryegrass synthetics

Factor level / coefficient	Herbage yield H1 (dt ha^{-1})	Herbage yield H2 (dt ha^{-1})
Ploidy		
2x ($n = 93$)	100.3	84.4
4x ($n = 73$)	108.8	95.3
p-Value	<0.0001	<0.0001
Time of inflorescence emergence (dt ha^{-1} d^{-1})	−0.254 ($p < 0.001$)	0.079 ($p = 0.250$)
Year of polycross (dt ha^{-1} yr^{-1})	0.233 ($p = 0.026$)	0.250 ($p = 0.026$)

p probability of error (F-test)

The analysis of DM yield data of the second harvest year (H2) showed the same trends (Fig. 2.2), but the relationship between size of the synthetic and performance was somewhat looser than that observed in H1. Irrespective of the regression model and the ploidy level, p (probability of error) values for H2 were always higher than those for H1, indicating a less good fit of the observed values to the model (Table 2.2). However, for the diploid synthetics, again, the hyperbolic regression yielded the lowest probability of error, hence the best fit to the model. Again, a large difference in behavior between diploid and tetraploid synthetics was observed, with the latter always being far away from statistical significance of the regression. The decline of performance with low numbers of parents of the diploid synthetics was consistent with the predictions of Posselt (2010), who found a marked decline below seven parents. When we analyzed subsets of our diploid data, the linear regression of H1 and H2 DM-yield on synthetic size became insignificant when synthetics with less than 7 (H1) or 6.5 (H2) parents were omitted (data not shown).

Contrary to expectations (Posselt 2010), no optimum number of parents for synthetics was apparent. This was mainly due to the lack of decline of DM yield with very high numbers of parents. Obviously, in the case of model experiments like those reported by Posselt (2010), the maximum number of parents possible is the number of genotypes actually present in the model set, which will include the poorest performing ones. In our practical plant breeding data set, even large numbers of parents still represent a restricted selected fraction of the total variation available.

The absence of a decline in performance with low numbers of parents at the tetraploid level is consistent with the data presented by Baert et al. (2007) who found a lesser importance of inbreeding depression with tetraploid than with diploid breeding material of perennial ryegrass. In tetraploids, the chance of having at least one positive (dominant) allele is

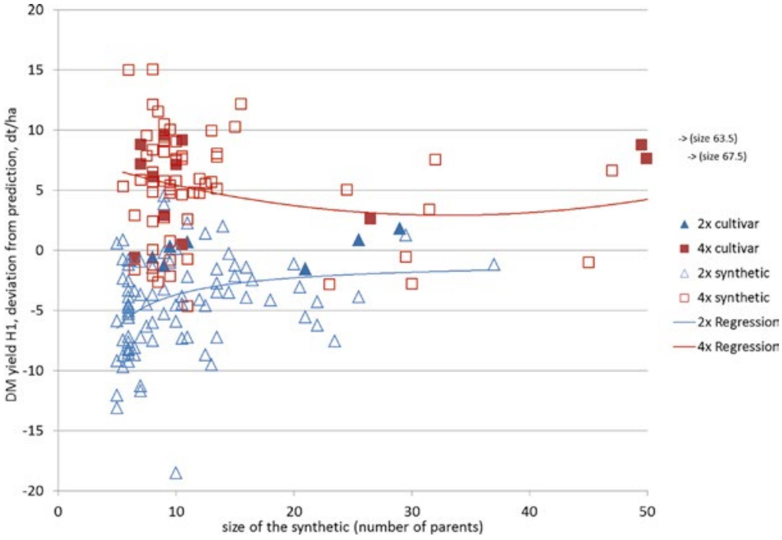

Fig. 2.1 Influence of synthetic size on total first harvest year (H1) herbage dry matter yield (deviation from prediction based on earliness and year of polycross) of 93 diploid (2x) and 73 tetraploid (4x) perennial ryegrass synthetics. Regressions according to the best solution of models summarized in Table 2.2 are shown

Table 2.2 Coefficients and statistical significance (*p* probability of error (F-test)) for different regression models describing the relationship between synthetic size (*n*) and total herbage dry matter yield (*Y*) of 93 diploid and 73 tetraploid perennial ryegrass synthetics

		Diploid (2x) synthetics				Tetraploid (4x) synthetics			
Model	Yr	a	b	c	p	a	b	c	p
Linear: $Y = a + b \times n$	H1	−6.24	.189		.0029	5.58	−.019		.672
	H2	−6.46	.189		.0145	5.52	.006		.897
Quadratic: $Y = a + b \times n + c \times n^2$	H1	−7.53	.405	−.007	.0077	8.04	−.310	.0047	.166
	H2	−8.40	−.010	.512	.0257	6.49	−.109	.0018	.755
Hyperbolic: $Y = a + b \times (1/n)$	H1	−.88	−28.1		.0006	4.06	12.7		.370
	H2	−.76	−31.1		.0018	4.86	7.44		.590
Logarithmic $Y = a + b \times \log(n)$	H1	−10.19	2.67		.0011	7.21	−.781		.418
	H2	−10.75	2.82		.0045	6.00	−.167		.859

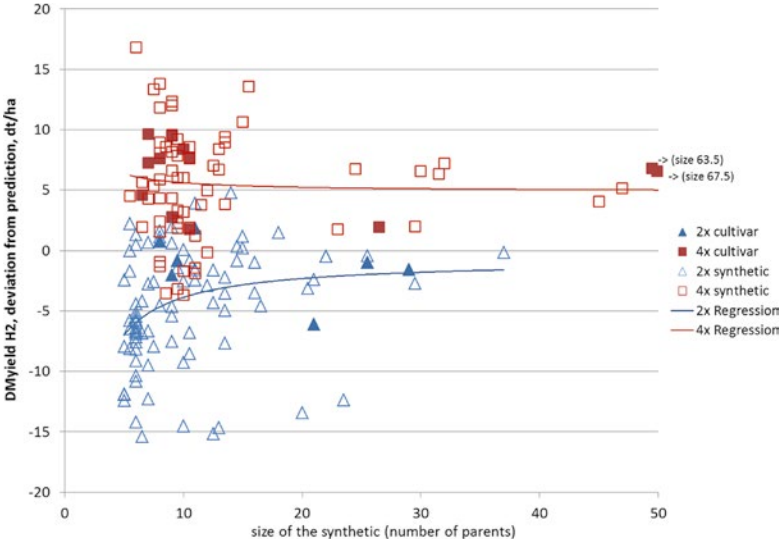

Fig. 2.2 Influence of synthetic size on total second harvest year (H2) herbage dry matter yield (deviation from prediction based on earliness and year of polycross) of 93 diploid (2x) and 73 tetraploid (4x) perennial ryegrass synthetics. Lines represent the hyperpolic regressions that showed best fit to the data (Table 2.2)

much higher than in diploids and, under a preponderance of digenic interactions, the observed lower inbreeding depression can be expected. Apparently, tri- and tetragenic interactions, which would lead to an increased inbreeding depression in tetraploids, are of low importance. This is in line with Gallais (2003), who reports a lower importance of tri- and tetragenic interactions for induced compared to natural tetraploids.

Conclusions

Based on the analysis of data from an actual breeding program, this study shows a clearly different behavior of diploid and tetraploid perennial ryegrass synthetics when considering the influence of synthetic size on performance. While the expected decline of herbage dry matter yield due to inbreeding depression was apparent when the number of diploid parents dropped below seven, no such decline was observed with tetraploid material. Indeed, selection intensity in tetraploid perennial ryegrass can be increased, at least down to five parents, without hampering dry matter yield of synthetics.

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Phenotyping Genetic Diversity of Perennial Ryegrass Ecotypes (*Lolium perenne* L.)

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Abstract

Perennial ryegrass (*Lolium perenne* L.) is the most valued temperate grass species in Europe. Between 2002 and 2010, a total of 352 *L. perenne* accessions originating from four European countries (Bulgaria, Croatia, Ireland and Spain) were evaluated in four phenotyping experiments at the Malchow experimental station of the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK). Ten plant parameters were visually scored, including development before and after winter, spring growth, plant biomass and incidence of crown rust and disease symptoms (leaf spot symptoms). Accessions from Croatia, Ireland and Spain were characterized by higher plant biomass in the 2nd scoring year than Bulgarian accessions. Considering the incidence of rust and diseases in perennial ryegrass accessions, the present study showed that the variation for scored crown rust and disease symptoms was higher in Irish and Bulgarian accessions. Correspondence analysis (CA) was carried out to examine the relationship between scored traits and 352 *L. perenne* accessions. The results presented in this study provide a brief description of *L. perenne* accessions maintained at the Satellite Collections North of the IPK Genebank.

Keywords

Perennial ryegrass accessions • Geographic origin • Genebank • Phenotyping • Correspondence analysis (CA)

Introduction

Perennial ryegrass (Lolium perenne) is one of the most valued temperate grass species in Europe. Especially its high productivity, nutritive value, digestibility and grazing tolerance makes it a valuable source for feeding livestock

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