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Review

Sustainable agriculture through perennial grains: Wheat, rice, maize, and other species. A review

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ABSTRACT

Grain crops are an important part of the human diet, accounting for a third of the consumed calories. Throughout human history, annual grain crops with high yields have been obtained through domestication. However, the "annual" characteristic brings associated a series of economic and environmental disadvantages, such as soil erosion or low soil resources use, that can be solved if the agriculture of annual varieties evolves towards perenniality. For this reason, there are numerous research groups dedicated to study and obtain perennial varieties of the most cultivated grain crops. In this review article, we have summarized the most important advances related to the subject, focusing on the domestication and hybridization of the most productive grains globally: wheat, rice, maize, rye and sorghum. We highlight their benefits for sustainable agriculture worldwide due to perennial grains may contribute to reducing erosion, acting avoiding carbon losses, reducing nutrient losses to waters or capturing nutrients deeper in soil when they are scarce, reducing farm costs and thus, increasing the effectiveness of agricultural grain crops. Despite perennial grain crops having disadvantages, they possess outstanding characteristics which make them resilient crops to deal with the imminent climate change. However, maintaining the perenniality trait without reducing genetic biodiversity is a great challenge of current scientific importance that must be deeply considered.

1. Introduction: intensive grain production

Human nutrition is closely related to grain consumption: rice, wheat and maize are three basic pillars of the human diet (Neumann et al., 2010), and about 35% of human's calories intake comes from these crops (Ross-Ibarra et al., 2007). Production of these three grains has increased greatly over the last 60 years (Fig. 1A): wheat and rice have tripled and maize has increased fivefold (FAO, 1997). Although production has increased, cultivated area has not grown in proportion, therefore the improvement in production must come from an increase in yield (Fig. 1B), associated with improvements in production technology, selection of higher-yielding varieties, and intensification of agriculture. Moreover, even though a greater amount of food is being generated than in any pastime, the agricultural practices that make this possible represent a serious threat to biodiversity and ecosystem functions (Cox et al., 2006).

Intensive grain production systems are based on monocultures, to which large quantities of fertilizers and pesticides are added, and which also need ample labor to prepare the land. These activities require high inputs, causing severe soil and environmental disturbance (Pimentel et al., 2012). One of the main problems associated with conventional agricultural production systems is water contamination, concretely groundwater, given the amount of pesticides and fertilizers added to the soils. For example, in the case of maize, wheat, and other grains, it is estimated that crops only take up to 50% of the supplied nitrogen (Cassman et al., 2002), and the remaining material ends up in the soil, waterways, and groundwater supplies. This is a remarkable problem, considering that about half of the world's population depends on groundwater for survival (Oki and Kanae, 2006).

Another of the worrying aspects of intensive systems is the reduction in biodiversity associated with the application of pesticides, mainly insecticides and fungicides, and with the extensive cultivation of genetically similar plants. This, together with the need for food supply for an ever-growing population, threatens biodiversity at unprecedented levels (Tilman et al., 2001). Climate change is also promoted by this type of agriculture. On the one hand, both pesticide and fertilizer production and agricultural management involve the use of machinery and fuel: some authors point out that more than 800 liters of petroleum are

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required to maintain the production of one hectare of maize (Pimentel and Patzek, 2008). On the other hand, soil management, added to annual crops with shallow roots, makes organic carbon more exposed to atmospheric agents, thus increasing the rate of oxidation and mineralization, increasing the rate of CO_2 released into the atmosphere (Lal, 2004).

Intensive grain crops also generate serious erosion to the soil system, often caused by water in areas with steep slopes that do not have vegetation cover or are subjected to ploughing processes. Tillage also promotes soil wind erosion which, despite not having the same global importance as soil water erosion (between 20 and 30 gigatons of soil yr^{-1}), is a serious problem that causes losses of about 5 gigatons of soil yr^{-1} (FAO, 2015). This soil loss is associated with a decrease in the organic matter content, nutrient depletion, alteration and destruction of the soil structure, and, in some cases, a decrease in production compared to non-eroded soils (den Biggelaar et al., 2001).

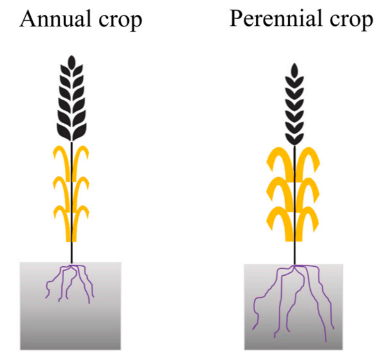
The disadvantages and problems due to intensive agriculture have made this production system unsustainable leading to the emergence of more environmentally beneficial alternatives such as conservation agriculture. This type of production is based on satisfying human needs for food, fiber and materials while maintaining the quality of the environment, making efficient and responsible use of potentially renewable resources, and reducing the amount of inputs as much as possible (Heslin, 2015). For instance, under conservation management systems and with the end to avoid soil loss, tillage practices are reduced and the period that soil remains covered is maximized by using forage crops, vegetable remains and perennial crops (Ghabbour et al., 2017). Therefore, sustainable alternatives must be adopted to combine agricultural development and environmental protection.

1.1. Introducing perennials: general pros and cons

Perennial crops would not need replanting –as the main characteristic– because they regrow after harvest. Consequently, production costs would decrease (e.g., lower seed costs) and field management tasks would be reduced (Zhang et al., 2018a, 2018b). By not disturbing the soil, perennial crops can favor soil biodiversity (McLaughlin and Mineau, 1995), providing, for example, additional niches for soil beetles (Burmeister, 2021). They allow the development of a more natural soil system and, presumably, with improved soil health, high drought resilience and long-term stability (Burmeister, 2021; Sanford et al., 2021). Additionally, considering the higher aboveground biomass production in perennial crops, the use of by-products such as mulch or husks can be increased (Fig. 2).

Perennial crops have been used as cover crops for years, due to their ability to reduce the amount of leached nitrogen and fix atmospheric N_2, stabilize soil, protect it from erosion and contribute to the development of its structure, improve soil health and increase carbon sequestration (Kaye and Quemada, 2017). Perennial species have a series of advantages over annual crops, since they tend to have more developed root systems (Fig. 2) that make them more efficient in nutrient uptake. The root system of perennial species could contribute not only to improve soil quality, but also to increase carbon sequestration and water infiltration (Snapp et al., 2019). Roots can make better use of soil resources and avoid nutrient loss by leaching (Jungers et al., 2019). This type of rhizosphere network is more interconnected and can form functional biopores larger than 40 cm. Thus, perennial crops can make better use of the water and nutritional resources provided by the subsoil, compared to a topsoil lacking or depleted of nutrients and/or water, a state caused by intensive agriculture or by the consequences of climate change (Glover and Reganold, 2010; Kautz et al., 2013). At the sustainability level, the attribute of perenniality means that perennial crops have access to nutrients for a longer time, which, if obtained via fertilizers, would reduce nutrient leaching and improve water quality, especially groundwater (Dance, 2017).

The current problem with most perennial grain crop varieties is that, given their characteristics, they could be used as forage or for biofuel production, but their yield is much lower than that of annual crops and their cultivation would lead to a reduction in annual grain production. Another potential problem associated with perenniality is the difficulty in introducing crop rotations, which would have to include long-cycle crops, displacing, as a consequence, other food crops. This could also



	Annual crop	Perennial crop
Average yield	+	-
Yield stability	-	+
Water requirements	-	+
Water productivity	+	-
By-products production	-	+
Soil stability and quality	-	+

Fig. 2. Comparative diagram of perennial and annual crop characteristics and requirements.
Figure adapted from Vico and Brunsell (2018).

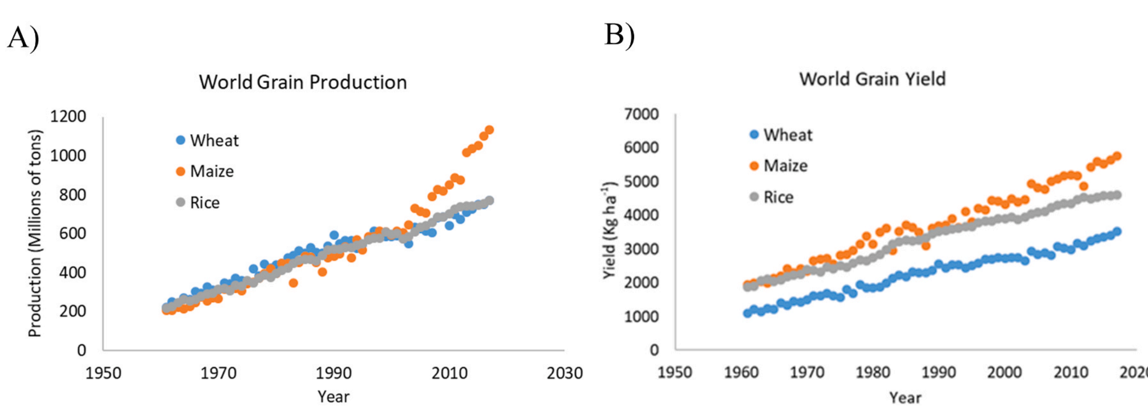


Fig. 1. World A) production and B) yield of three grain crops (wheat, maize and rice) between 1961 and 2017 (FAO, 1997).

lead to a greater pest potential by hosting a higher number of pathogens, pests or weeds, which would be favored by the lack of soil tillage and pesticide treatment (Shim, 2012).

Concerning soil fertility, in the absence of tillage and in soils with low organic matter, plants with a highly developed root system can accumulate a high carbon content to such an extent that nitrogen and phosphorus imbalances may occur (Qaswar et al., 2019). However, in the case that perennial crops need nutritional contributions, these inputs will be better used given the capacity of their root system to capture nutrients.

Considering how beneficial it would be to switch from an annual to a perennial crop, they deserve special attention. Consequentially, in many countries there are programs to create hybrids or perennial grain varieties of crops such as wheat, rice, sorghum, oats and barley (Kantar et al., 2016).

In this review article, we will focus on: i) characterizing the advances made in recent years to obtain new species and varieties of perennial grain crops and, ii) the possibilities they offer for a future marked by a trend towards environmental conservation: establishment of perennial grain cover crop systems, better use of soil resources (water and nutrients), soil protection against erosion (both water and wind), development of a complex structure, reduction of tillage and soil biodiversity increase, among others. We will analyze the strategies used to obtain new perennial crops and the aspects that make these crops ideal candidates for soil recovery or for improving soil health and its biodiversity.

2. Perennial crops: an overall perspective

2.1. Reference search

To assess the available literature regarding perennial grains, the search was conducted in SCOPUS, SCIENCEDIRECT, WEB OF SCIENCE, GOOGLE and GOOGLE SCHOLAR. The total citations obtained were 153, including 137 research papers, 6 research books, 9 webpages and 1 statistics database. In the analyzed works, information about the following perennial crops was sought: wheat (31 studies), rice (21 studies), maize (10 studies), rye (7 studies), and sorghum (4 studies). Additionally, we extrapolated information about "perennial crops" or "perennial grains" from 32 studies, and 38 studies were considered of general areas related to the topic, such as agriculture, environment, ecology, breeding, and botany, among others.

To obtain the articles cited in the reference list, we used the following keywords and combinations of the same words using "AND": "perennial", "grains", "wheat", "rice", "maize", "(winter) rye", "sorghum", "crops", "breeding", "agriculture", "environment", "ecology", "market", "production", "domestication", "hybridization", "annual", "agroecosystem", "Kernza", "ratooning", and "*Thinopyrum intermedium*". The period covered by the review ranges from the late 20s of the 20th century, concretely 1929, until August 2021.

2.2. Selection and hybridization

Since 10,000 years ago, when the first farmers appeared, arable land has been largely devoted to producing annual crops (Cox et al., 2002). Seeds of such crops, being larger and capable of germinating and developing quickly, spread rapidly throughout Asia during the droughts that occurred at the end of the Pleistocene ice age (Whyte, 1977).

In the 20th century, agriculture based on annual crops was pushed to the extreme to feed a growing population, and this has generated a loss of soil due to erosion, a problem that some authors quantify at one-third of the arable surface of the planet (Pimentel et al., 1995). The necessary change towards a more environmentally friendly agricultural production system has a branch devoted to the development of perennial crops that can be used for human consumption. Depending on the crop type, one path or another is followed. For example, some perennial crops such as intermediate wheatgrass have a high yield and, although it is not comparable to the production of annual wheat cultivars, through a selection (or domestication) program, varieties with greater productions are being obtained. Domestication can be explained by two different hypotheses (DeHaan et al., 2020). The first maintains that the domestication of wild species is produced by the alteration of genes that already exist in natural varieties (tinkering) (Doebley, 2006). That is, there is no addition or depletion of genes, but the characteristics that make a species suitable for cultivation are achieved through mutations. The second hypothesis maintains that domestication is based on the loss of certain genes that make species suitable for production but, at the same time, makes them lose competitiveness in natural environments (Østerberg et al., 2017). Therefore, domestication is a consequence of both natural (unconscious) and artificial (scientific and conscious) selection (Van Tassel et al., 2010). On the other hand, interspecies hybridization between annual crops with perennial ones may occur. For instance, rice and sorghum can be combined with close perennial relatives, but other crops such as maize or wheat need to be hybridized with perennial species belonging to other species or genera (Cox et al., 2002; Kantar et al., 2016).

However, considering the successful development recently occurred about genome editing and the big data analysis, some authors conclude we are on the threshold of a new generation-plant breeding, and that will help to develop adapted crops fulfilling demands of the local population, the climate and the conditions of specific areas of the planet (Wallace et al., 2018). Some progress has already advanced in gene editing of annual crops using CRISPR/Cas techniques (Ricroch et al., 2017), especially with rice, tomato, maize, potato and wheat species. Fernie and Yan (2019) indicate that such developments should be focused on obtaining perennial crops that make good use of water and nitrogen, have tolerance for contaminated soils, and produce food with high nutritional quality.

2.3. Perennial plants cycle

Perennial crops are composed of plants that do not die after harvest. They can flower throughout the year or show temporary flowering, which occurs through vegetative growth (Albani and Coupland, 2010). Perennials are divided into two types: simple and progressive ("creeping"). Their growing cycle, in a simplified way, is compared to that of the annuals in Fig. 3.

- Simple perennials reproduce by seeds and by vegetative or asexual reproduction, which is considered an agronomic technique producing plants genetically identical to the mother plant. They come up from a cell, tissue or organ of the mother plant. However, the usual mode of reproduction is through seeds.
- Some creeping perennials reproduce by seeds or by vegetative reproduction of organs. These can be both aerial stems (stolons) and underground tubers (specialized rhizomes) or bulbs (Zimdahl, 1993).

Once perennial plants reach the vegetative stage, they can be monocarpic, i.e., they spend more than 1 year in a vegetative stage before flowering once and then die (Jørgensen and Fath, 2008); or polycarpic, i.e., they can reproduce more than once before dying by retaining, at least, one meristem in the vegetative stage after flowering (Albani and Coupland, 2010).

3. Wheat

Numerous research programs are currently dedicated to obtaining perennial wheat species, often through domestication of wild perennial species or interspecies hybridization.

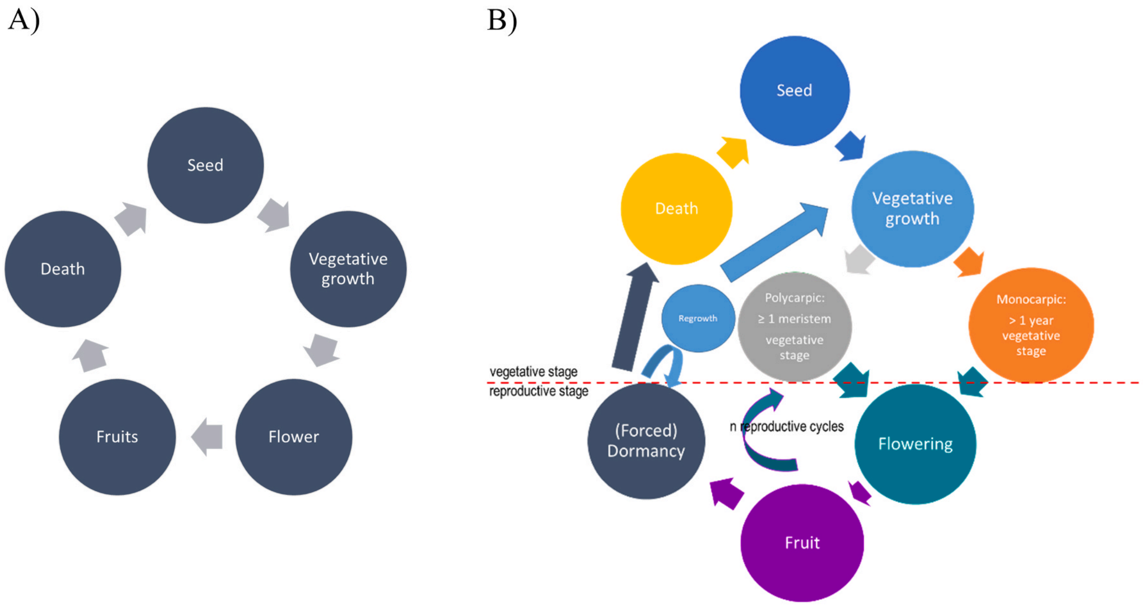


Fig. 3. A) Annual plant growing cycle compared to B) (simplified) perennial growing cycle. Adapted from Zimdahl (1993) and updated from Duchene et al. (2021).

3.1. Selection of interesting varieties for domestication

There are three perennial species capable of hybridizing with annual wheat that, due to their characteristics, are good candidates for domestication (Cox et al., 2002): lyme grass (*Leymus arenarius*), mammoth wildrye (*Leymus racemosus*) and intermedium wheatgrass (*Thinopyrum intermedium*).

Leymus arenarius (Fig. 4) is the most common lyme grass species in Europe. It is found in Central Europe, England, Scotland, the Faroe Islands, and Iceland, and it colonizes northern Russia, Scandinavia and the countries around the Baltic Sea (Anamthawat-Jónsson et al., 1994). Given its ease of growing in extreme environments, such as sandy soils or dunes in coastal areas with high concentrations of salts, where common wheat does not usually settle, *Leymus arenarius* is a species that offers great potential to be domesticated, or even included in hybridization processes of common wheat, to give it greater resistance to cold or salinity (in addition to the perennial characteristic). Each plant produces a high number of grains (from 200 to 300), and high-quality seeds with high-protein content. Furthermore, it is a species that has been used for over a century in extreme climates (such as Iceland) for the stabilization of drifting sands and eroding fronts (Greipsson and Davy, 1994).

Leymus racemosus (Fig. 5) is a perennial species that grows on islands

Fig. 4. *Leymus arenarius*. Image from Krzysztof Ziarnek (2018).

Fig. 5. Image of *Leymus racemosus* from Krzysztof Ziarnek (2018).

or in dry coastal areas of Europe and Asia (Kishii et al., 2004). This species has a great growth manifested by long roots and stems and large ears. *L. racemosus* tolerates hot, dry and saline environments, and soils with high aluminum concentrations. It has been used to stabilize soils, protect dunes, or create habitats for animals. This species can be used for grain production in soils unsuitable for cultivation due to its high tolerance to extreme conditions. Despite being evolutionarily distant from wheat, this species can hybridize with it and improve it since, in addition to the aforementioned tolerances, *L. racemosus* shows resistance to scab (*Fusarium* head blight) (Mujeeb-kazi and Rodriguez, 1981). Moreover, exudates from its root system are capable of inhibiting biological nitrification and thus, preventing consequent nitrogen loss (Subbarao et al., 2007).

One of the most promising candidates for domestication is *Thinopyrum intermedium* (Jungers et al., 2018), a cool-season perennial with tall growth, long roots and large seeds. It is native to Eastern Europe and Western Asia, and given its high biomass production, it has been used to produce forage in North America and other temperate regions (Jensen et al., 2016). Domestication of this species has been done through selection, trying to reduce the plant height and increase its yield (by increasing the seed size and the protein content, obtaining more seeds per plant and reducing the shattering, among others) (DeHaan and Ismail, 2017). Furthermore, it is considered the closest perennial relative to common wheat (*Triticum aestivum*) (Zair et al., 2018).

Currently, there is a *Thinopyrum intermedium* variety trademarked under the mark name Kernza®, that has been developed by The Land Institute, a non-profit organization devoted to sustainable agriculture (Salina, Kansas, USA) (de Oliveira et al., 2020). Kernza® is starting to be used in restaurants, bakeries and the brewing industry (Ryan et al., 2018). In addition, it has been shown that this crop reduces NO_3^- leachates, increases the labile fraction of C in the soil, and can make better use of soil moisture since its roots penetrate deeper layers (Culman et al., 2013). More recently, it has been developed the world's first commercial food-grade intermediate wheatgrass grain cultivar named as MN-Clearwater' (Reg. no. CV-287, PI 692651), developed by the University of Minnesota (Bajgain et al., 2020), showing there is still a long way to explore regarding this grain.

3.2. Wheat hybrids: a global perspective

There is a wide range of perennial species of the *Triticeae* tribe, such as wheat (*Triticum*), wheatgrass (*Thinopyrum*, *Agropyron*), goatgrass (*Aegilops*), rye (*Secale*), wildrye (*Leymus*, *Elymus*) and barley (*Hordeum*), which have been used to achieve a perennial hybrid of common wheat during the 20th century. However, only wheat hybrids with certain resistances (winter hardiness, and resistance to diseases and drought) were successfully obtained (Wagoner, 1990). As mentioned in the previous section, plants derived from *Thinopyrum* spp. are the most interesting given the good affinity between these species and common wheat (Li et al., 2008), and the ease with which they produce fertile hybrids (Cox et al., 2002).

There are currently more than forty research centers around the world, in countries such as the United States, Argentina, Turkey, China, Germany, India or Australia, that are dedicated to research on perennial grain crops (Crews and Cattani, 2018). In one of the largest studies developed with perennial wheat, whose experiments were carried out using various perennial hybrids in nine countries of four continents (Hayes et al., 2018), it was observed that those plants derived from *Thinopyrum intermedium* (*Triticum* spp. × *Thinopyrum* spp.) offered better yield and greater resistance in high latitudes (Sweden and Canada). However, the most productive hybrids at low latitudes ($< 41.57°$) were those obtained with *Th. ponticum* and *Th. elongatum*.

In China, hybridization of wheat with species such as *Th. ponticum*, *Th. elongatum* and *Th. intermedium* has also been studied since the 1950s (Cui et al., 2018). The most promising hybrids are those with *Thinopyrum intermedium* since, apart from the perenniality characteristic, the resulting plants have multiple ears and the grains pose high-protein content. These hybrids were able to resist cold temperatures (- 20 °C) and, as in the case cited above, some of them showed resistance to the fungi causing wheat rust and powdery mildew, as well as to cereal cyst nematode (Bell et al., 2010).

In Australia, there exist two native perennial species that can hybridize with common wheat: first, *Elymus scaber* is a widespread plant capable of hybridizing with barley, wheat and rye (Torabinejad and Mueller, 1993); and secondly, the *Australopyrum* species, much less common. Additionally, those of the genus *Thinopyrum* are interesting plants because of their abundance and morphology: there are about four species of this genus spread across the country and, given their extensive root system, they are valid candidates for coping with the drought stress suffered in a big part of Australia (Fedak, 1985).

3.3. Wheat hybridization: tools and challenges

As mentioned above, hybridization between perennial and annual species is a technique often preferred because it is not as time-consuming as selection, but presents several challenges. For example, the number of chromosomes or sets of chromosomes do not usually coincide in the parental species, or do not recombine during meiosis (Crews and Cattani, 2018); infertility often appears in hybrids, or the seed number is frequently reduced (Hayes et al., 2018). Thus, perenniality trait is difficult to maintain.

The perennial species of the *Triticeae* tribe are suitable candidates for hybridizing with wheat (Cui et al., 2018). In previous sections, it has been stated that *Thinopyrum spp*. are the most interesting since they are species that have been studied for a long time (Li et al., 2008) and they are easy to hybridize with *Triticum* species. Up to date, the genes responsible for the perennial characteristic of wheat have not been located. However, in the study carried out by Hayes et al. (2012), in which 150 wheat × wheatgrass (including *Th. ponticum* and *Th. intermedium*) hybrids were examined, the results showed that those species, which successfully re-sprouted after harvest, had about 56 chromosomes in their genome, i.e., 14 more than common wheat.

Genetic sequencing experiments are currently being carried out to develop selection and hybridization programs (Cui et al., 2018). For example, Zhang et al. (2016) analyzed the genome of *Th. intermedium* to search for genetic markers that can be used to predict the effect of certain genes, and thereby improve recurrent selection. Other authors have gone a step further: since 2019 there is a high-quality genetic map of this species (available online: Dorn and Poland, 2019). The species *Th. intermedium*, like common wheat, is segmental autoallohexaploid ($2n = 6x = 42$), so that an individual has six alleles of a similar gene (Mahelka et al., 2011). When establishing a hybridization program, this complicates matters, especially if the mutated gene that produces the desired phenotype has a recessive character, since it must be ensured its presence on the six chromosomes that encode it (DeHaan et al., 2020).

When developing new wheat species (perennial or annual), a series of characteristics are sought. The most common is looking for hybrids that have a certain grain size, which (in wheat and rice) is related to the GARS7 gene (Dong et al., 2014), or plants with many ears and many seeds. The latter trait is regulated by the GNI1 gene (in wheat and barley) (Sakuma et al., 2019). In the case of wheat and rice, which are not grown for forage, it is also interesting to obtain short crops since they are less sensitive to climatic conditions. In the 1960s, two genes that caused a large increase in production were introduced: Rht-B1 and Rht-D1 genes (two mutant forms of the Rht-1 gene) (Jobson et al., 2019). These mutated genes reduced crop height by reducing the response of wheat to gibberellin (Peng et al., 1999).

The desired characteristics of perennial, annual or hybrid crops can be achieved through gene-editing (or genetic engineering), that is, using technologies that precisely allow alterations to be introduced into the genome of organisms (Kumar et al., 2019). These modifications include deletions, insertions, substitutions or mutagenesis targeting specific parts of the genome (Zhang et al., 2018a). First-generation gene-editing techniques, based on engineered endonucleases, have been widely used with common wheat to breed powdery mildew-resistant wheat varieties (Wang et al., 2014). These techniques are expensive and have certain limitations, which is why nowadays second-generation gene-editing techniques are preferably used, the so-called CRISPR (clustered regularly interspaced short palindromic repeats)/associated nuclease Cas9 (or CRISPR/Cas9), that are simpler and more effective (Wang et al., 2018). CRISPR/Cas9 techniques involve the Cas9 nuclease guided by an RNA strand that cuts the DNA double-strand.

Wheat is a challenge for editing: it is allohexaploid, with genetic material from three different species, and its genome is huge (17 gigabases), containing innumerable repetitions. However, promising work has already been carried out with this species to eliminate a specific gene in cell cultures (Upadhyay et al., 2013), or to introduce genes in the three homoalleles that give wheat resistance to powdery mildew (Wang et al., 2014). Wang et al. (2018) went one step further and managed to introduce heritable mutations in the TaGW2, TaLpx-1, and TaMLO genes, obtaining wheat plants that had larger grains. Considering these advances and the similarities in the genomes of *Triticum aestivum* and certain perennial species, such as *Thinopyrum intermedium* (DeHaan et al., 2020), it is possible to get soon a commercial perennial hybrid of common wheat.

Despite all difficulties provided for both strategies, domestication and hybridization, the last one is more promising since it is faster and allows combining the perennial characteristic with other desirable properties like grain quality (Cui et al., 2018). However, as mentioned above, the current challenge relies on maintaining the perenniality trait which is, perhaps, more important than the trait development.

3.4. Potential advantages and disadvantages of perennial wheat cultivars

Perennial wheat varieties could provide grain, forage, fuel and other bioproducts while contributing to resource conservation (Cox et al., 2006; Cui et al., 2018). The roots of intermediate wheatgrass are longer than those of annual wheat, reaching > 160 cm depth in two years (Duchene et al., 2020). In a comparative study between annual and perennial wheat, it was found that the perennial crop maintained the amount of phosphorus, both from the soil (native) and from fertilizers, in bioavailable forms, even at depths greater than 70 cm (Crews and Brookes, 2014). Recently, Sakiroglu et al. (2020) demonstrated that agronomic management, such as N fertilization and harvesting forage in a Kernza dual-use system, is not detrimental to intermediate wheatgrass above- and belowground productivity, maintaining environmental advantages for grain and forage production. In addition, considering the characteristics of perennial species (such as *Leymus racemosus*), they could be grown in extreme conditions, such as coarse textures, salinity or high latitudes. The implantation of these crops would reduce erosion for years mainly due to their rhizosphere development, allowing the soil structure to develop under a cover that would be maintained for most of the year (Cui et al., 2018). A recent study where salinity was tested also revealed that a perennial wheat-based crop resulted in salt-stress tolerance with a small decrease in biomass production, making it suitable for production in arid climates and salinized soils as forage (Abbasi et al., 2020). Another advantage of perennial wheat cultivars is that they attract farmers' interest, according to a series of surveys conducted in France and the United States (Wayman et al., 2019). The main reason for this was related to the improvement of soil health and the associated economic benefits because of their dual use.

However, despite presenting agronomic and environmental advantages, perennial wheat varieties are crops that present certain disadvantages. For example, they can store diseases for several years due to their establishing (Wayman et al., 2019). This is not an exclusive problem of wheat and affects most perennial species, since rotations cannot be made, and this is one of the best strategies to cope with pests (Cox et al., 2005). However, it is important to note that perennial crops also increase the amount of organic matter in the soil (Gebhart et al., 1994) and enhance the development of soil biodiversity (Piper, 1996), establishing competitive relationships and preventing the excessive proliferation of certain diseases. For instance, root fungi such as *Rhizoctonia solani* AG3 are suppressed in grasslands (Van Elsas et al., 2002). Perennial wheat varieties are crops that need time to develop their tissues and roots, so they tend to delay seed production (Jaikumar et al., 2014). In fact, perennials produce similar root biomass to annual wheat in its establishment year. Recent studies have observed that their root expansion does not occur until the regrowth period (Duchene et al., 2020), and that makes the further expansion is still additional without the potential loss of sequestered carbon as in annual cropping systems. Although they present a more stable yield, perennial wheat crops tend to produce a lower amount of grain and require greater amounts of water (Vico and Brunsell, 2018). However, the latter may become an advantage in temperate zones that have a high humidity regime, considering not only their water consumption but also the increased infiltration that their root system brings, making them crops with better and more efficient use of year-round precipitation (Scheinost et al., 2001). For instance, perennials are able to trap snowfall as cover in some growth environments, which retains moisture in the area, unlike happens on annual cropped lands.

4. Rice

As mentioned in previous sections, rice production has tripled in the last 60 years (Fig. 1). Regarding the acquisition of perenniality, the case of rice is simpler than that of wheat since, although it is usually grown annually, many rice cultivars are perennials (Sacks, 2014). If the *Oryza sativa* species is provided with the right humidity and temperature conditions after harvest, it will produce new spouts and a new crop, through a process known as ratooning (Hill, 2010). This practice has aroused the interest of both farmers and researchers in recent years.

Early studies on the subject concluded that rice was domesticated in swampy areas of Southeast Asia, near the Bay of Bengal, where numerous wild varieties of rice coexisted (Sacks, 2014). However, more recent research has determined that the earliest rice cultivation came from the Yangtze region of China, where archaeological evidence of cultivation is about 10,000 years old (Jiang and Liu, 2006). Although there is still no consensus on when domestication occurred, it can be concluded that there was a genetic alteration that turned wild rice into domestic rice through the loss of the seed shattering trait (Sang and Ge, 2007). This is a trait that facilitates harvest, and that also differentiates wild and domestic rice varieties (DeHaan et al., 2020).

There is considerable consensus about the fact that both domesticated rice varieties (*O. sativa*, in Asia, and *O. glaberrima*, in Africa) are derived from perennial ancestors (Cheng et al., 2003). In the case of *O. sativa*, it is believed that comes from a species known as *O. rufipogon*, which can be subdivided into four clades, three of which are perennial. It has been found that the *japonica* subspecies of *O. sativa* comes from one of these perennial clades, while *O. sativa indica* comes from the annual O. *rufipogon* clade (Cheng et al., 2003). For this reason, *japonica* cultivars have been found to be more prone to ratooning, and it is the variety used, for example, in the southern United States for larger-scale production (Lu et al., 2005).

There are certain differences between the regrowth of wild species and domesticated rice: while the latter regrows through tillering, that is, new buds grow on old tillers, *O. longistaminata* produces rhizomes and *O. rufipogon* perpetuates itself through spurs (Sacks, 2014).

4.1. Strategies to focus the development of perennial rice crops

4.1.1. Improving ratooning technique

Even though ratooning is a process that occurs daily with *Oryza sativa*, it needs to be improved as ratooning currently produces only 40% of yield compared to the first harvest. This yield is even reduced with each harvest, making this system not economically viable if compared, for example, with double-season rice (Dong et al., 2017), i.e., one variety that allows two harvests per cycle. However, there are certain genotypes that, depending on climatic conditions, are capable of generating a higher yield, so the selection of the right variety can be a good system to deal with low yields. The selection of those species or cultivars whose regrowth and production are little affected by drought or cold is also of interest (Sacks, 2014). Yuan et al. (2019) have observed that ratooning produces lower yields than double-season rice (around 13% lower), but the energy consumption required using this system is 32% lower. In addition, this method is 40% cheaper (as it does not require replanting) and thus, is much more environmental friendly when considering the CO_2, CH_4, and N_2O emissions per kilogram of rice produced.

4.1.2. Introgression of genes from perennial crops into O. sativa

The addition of genes from its perennial relatives to the *O. sativa* genome is another option to improve the capabilities of this species and achieve a perennial hybrid. *O. rufipogon* is a good option given its high genetic compatibility with common rice, but its year after year perpetuation form, spurs, may not constitute the best procedure to reach perenniality since they are more susceptible to drought than rhizomes of *O. longistaminata*. In addition to this advantageous characteristic, *O. longistaminata* is capable of developing wild monocultures, is diploid like common rice and has the same number of chromosomes (Zhang et al., 2014).

The first perennial hybrid between *Oryza sativa* and *Oryza longistaminata* was obtained in the year 2000 (Dayun and Sripichitt, 2000). For the successful generation of a perennial hybrid, it was necessary to perform intercrosses in the first offspring generation (F1) as well as backcrosses with one of the parents (*Oryza sativa*). Since then, five perennial hybrids have been obtained, named PR23, PR57, PR129, PR137 and PR139. The first of these lines (PR23) is the most promising and was obtained from the annual rice variety RD23. It was grown in both high and lowland areas, had a high yield, and produced good quality rice. In preliminary field studies, it has been determined that PR23 is capable of re-sprouting, and producing grain for at least three seasons. Huang et al. (2018) have observed that PR23 has a similar yield to that of the best annual crops (RD23 and HXR7), both in weight and quality, and generates great interest among farmers given the reduction in production costs. In addition, it has added ecological advantages such as soil stabilization since it is successfully produced under a no-tillage system. The latest published studies on PR23 explain how perennial rice responds to this new system: Zhang et al. (2021) suggested an innovative management scheme consisting of reducing N fertilization and increasing plant density. Their results enhanced the sustainability of the grain yield providing optimal conditions, both economically and environmentally.

4.1.3. Domestication of wild Oryza species

Domestication to improve crops is a technique that has an important disadvantage compared to the introgression of genes from other species: it is a slow process. Interesting genes for domestication appear in low frequency in parental populations and are usually recessive (Sacks, 2014).

As explained above, *O. longistaminata* is a great candidate for hybridization with *O. sativa*, but it is also interesting for breeding, as it is a perennial plant that can withstand drought. Another species that has similar characteristics is *O. australiensis*, but it is not as genetically similar to common rice, so it is more feasible to domesticate it than to hybridize it with *O. sativa*. Despite this, some hybrids of these two species have already been obtained by young embryo rescue (Yi et al., 2018). *O. australiensis* is a native species to northern Australia that has short kernels with high amylose content and high gelatinization temperature (Henry, 2019). In addition, this species has a certain tolerance to salinity (Yichie et al., 2018), and using backcrossing has allowed to grant resistance to brown planthopper (Jena et al., 2006), and bacterial blight (Brar and Khush, 1997).

When domesticating both species (*O. longistaminata* and *O. australiensis*) would be necessary to look for an improvement in yield, a decrease in height, and some system to control their invasiveness. With these considerations in mind, hybridization is more promising than domestication, as in the case of wheat.

4.2. Advantages and disadvantages of perennial rice

4.2.1. Advantages

The root system of perennial rice, in addition to improving soil structure, is more resistant to nematodes (Huang et al., 2018) and more tolerant to drought since it can make better use of water resources. Therefore, it requires a lower amount of irrigation and could be grown in areas with dry climates (Sacks, 2014). In addition, perennial rice cultivation requires less and lower tillage intensity, which could lead to a decrease in fertilizer application and crop inputs (Shim, 2012).

From an agronomic point of view, a great advantage to highlight is that it does not require tillage after the first transplanting and, consequently, reduces considerably soil exposure to erosion and the resulting negative impacts of tillage on soil structure.

Annual rice is grown in marginal areas with steep slopes without terracing, especially in Asian and African regions, becoming one of the biggest environmental problems of this crop. That makes soil loss up to 20 times greater than the rate of new soil formation. Growing perennial rice in these areas may represent an important advance for soil and habitat conservation, since the root development of perennial rice plants can significantly increase soil retention in its rhizosphere (Bird, 2015). By having a crop throughout the year, the ecosystem is stabilized, reaching a balance among all its members. This can result in a reclaim for pollinators, which have a fundamental role in crop productivity and increase the biodiversity of the habitats in which they are found (Werling et al., 2014). All these issues make perennial rice cultivation reach a balance between environmental protection, economic development and food safety, so its development involves green technology at agricultural level.

4.2.2. Disadvantages

Rice production through the ratooning technique is drastically reduced in the second year of harvest: they only reach 10% of the initial production (Sacks, 2014), although in certain varieties the yield may reach around 50–60%. This is because the species has been subjected to strong pressure from farmers towards the achievement of annual varieties (Hill, 2010). Weeds development is also a problem associated with rice regrowth. This makes it impossible to obtain crops beyond three consecutive seasons if there is not enough water, since weeds are controlled by flooding the land (Prashar, 1970). Such continuous exposure to water can lead to increased abiotic stress for the plant and nutrient deficiencies due to changes in conditions affecting microorganisms responsible for their fixation (Fukao et al., 2019).

5. Maize, rye and sorghum

5.1. Perennial maize

5.1.1. Beginning of the perennial maize

Murray and Jessup (2013) have intensively reviewed how perenniality has arisen in maize plants. In brief, domesticated perennial varieties of maize arose from crosses between common maize (*Zea mays*) and wild perennial species (*Z. perennis*, tetraploid – Mexico or *Z. diploperennis*, diploid – Mexico). The first known crosses were made at the beginning of the 20th century by Emerson (1929) and Mangelsdorf and Reeves (1939). The experiments carried out by the latter included *Z. mays* crosses with *Z. perennis* and *Tripsacum* (a genus grass) a perennial Eastern gamagrass adapted to temperate climates. The third generation of perennial genes was obtained from them. Years later, Mangelsdorf and Reeves continued with several *Z. perennis* crosses and other maize varieties, obtaining diploid and tetraploid varieties. After several crosses of both, diploid and tetraploid varieties, perennial varieties were achieved in 2009. However, these plants did not survive after extreme weather conditions. Through successive crosses was possible to obtain varieties with greater ear size and productivity, crucial parameters for the implementation of perennial varieties at agricultural level. During all these tests was observed that parameters such as tillering, stem tissue totipotency and delayed or eliminated senescence, needed to be improved to have a domesticated perennial maize variety. Despite this, plants left in the field as perennial variety trials did not survive drought, extreme heat, or frost, while *Z. diploperennis* plants survived for four years in a row. Therefore, it can be concluded that the species *Z. diploperennis* is an optimal candidate for further breeding to obtain a domesticated perennial variety with optimized agronomic parameters and economic importance. More recently, it has been shown that the *Z. diploperennis* species is resistant to seven viruses that attack annual maize, revealing that it may enrich the maize sector by generating around 4.4 billion additional dollars (Shand, 2020). However, Yan et al. (2020) have recently developed a specific trihybrid involving tetraploid *Zea mays*, *Tripsacum dactyloides* and *Zea perennis.* It is called Tripsazea: it is perennial, male-sterile and partly female-fertile. Tripsazea has a higher chromosome number, higher seed setting rate, and vegetative propagation ability of stand and stem. This trihybrid is a promising material to continue gene crossing into perenniality to improve maize traits.

5.1.2. Challenges to be achieved regarding the traits of perenniality in maize

Some important aspects to achieve when developing perenniality in maize are i) not showing senescence at the end of the season or being able to resprout after the season; ii) having resistance to frost (freezing) and extreme environmental conditions; and iii) to remobilize energy from hibernating structures for new growth in the spring (Murray and Jessup, 2013). All these characteristics would make the regrowth trait optimized to improve its genetic lineage and obtain better productivity and, thus, be agro–economically profitable. As an attempt, a study showed that F2 plants from crosses between *Z. diploperennis* and *Z. mays* identified that only a few individuals had identifiable rhizomes, explaining only 12% of the variance (Westerbergh and Doebley, 2004). This implies that the genetic results of F2 have low "inheritance", i.e., there are genes that are not optimal for being genetically reproduced. However, the results of crosses between maize and perennial sorghum explained a higher variance, close to 50%, with the genesis of rhizomes being more robust than those obtained only from the *Zea* genus (Murray and Jessup, 2013). In a recent study, Ma et al. (2019) have reciprocally crossed the perennial *Zea diploperennis* with annual *Z. mays* to study the regrowth trait. They have observed several cycles of growth, flowering, and regrowth in F1 plants with normal flowering, denoting a clear dominance of the perennial alleles. The ability to regrow after senescence (regrow-ability) was transmitted to the F2 plants. Furthermore, this is thought to be affected by other factors or environmental conditions. Genome-wide screening with genotyping-by-sequencing technology used in that study showed two major regrowth loci. This means that using the appropriate genetic technology, no barriers would be to transmit the regrowth trait between varieties of the *Zea* genus or other grasses to develop perenniality properly. Improving the regrowth trait has several agronomic and environmental advantages such as reducing soil erosion, increasing soil carbon sequestration and accumulation, and providing raw materials for both food and biofuels (Murray and Jessup, 2013). Conversely, Bernal et al. (2019) recently showed that the domestication of maize, both annual and perennial, alters the interactions between the crop and insects, such as maize leafhopper, which may increase its ability to produce a pest in the crop, resulting in a significant agro-ecological disadvantage.

According to Murray and Jessup (2013), other traits that perennial maize must achieve to improve perenniality are:

- Later canopy cover: greater foliage development would expand the canopy of the plants, increasing their surface area for capturing sunlight, optimizing the transformation of useful biomass. This trait has been observed by Murray and Jessup (2013) in perennial maize plants through greater foliar development and even stems and tillers.
- Delayed senescence or non-senescence: in crosses obtained from perennial varieties, a longer plant time in the green stage or delayed senescence has been observed, associating it with increased stress tolerance (Sade et al., 2018), leading to longer grain filling time. This trait is especially sought after in arid climates.
- Prolificacy: the ability to produce more ears per plant. Perennials tend to have multiple ears on each stem, or more stems with at least one ear. This is one of the most important traits due to the relatively positive correlation with grain yield (Bisht and Mani, 2016).
- Ear forest: some plant varieties tend to produce ears at the base of the plant, so an increase in this type of basal production could be used to feed the livestock that can digest it.
- Deeper rooting: an increase in root development of maize plants would favor a greater nutrient uptake, as well as greater soil fixation. This would favor its retention, so it would serve to recover degraded areas, for example, burned forest areas that may have potential use as agricultural land.

5.1.3. Gaps in perennial maize adaptation to edaphoclimatic conditions

Maize (*Z. mays*) requires high doses of lighting, is a fast-growing crop that yields at moderate temperatures, between 24 °C and 30 °C, as long as it has access to an adequate supply of water. Therefore, yields increase when grown in the rainy season or under irrigation. Maize adapts to a great variety of soils, with a preference for loamy and fertile soils. Compared to other crops, maize adapts to the soil acidity or alkalinity and can be grown with good results with pH ranging between 5.5 and 7.0, although the optimum corresponds to a slight acidity (pH between 5.5 and 6.5) (Silva, 2019).

Maize is considered moderately tolerant to salt content in soil or irrigation water, with the upper roots part being the most sensitive zone to the effects of salts: roots are more affected by salts than the aerial part (Silva, 2019). However, what kind of edaphoclimatic adaptations does perennial maize have compared to annual maize? What are the agro-ecological differences of its cultivation in the face of imminent climate change? Currently, little is known about the edaphoclimatic advantages of growing perennial versus annual maize. Few studies have been carried out to scientifically answer these questions. *Zea perennis* is known to possess genes conferring resistance against biotic and abiotic stresses, as well as adaptation to flooding and aluminum toxicity in soils (Iqbal et al., 2019). This, added to its adaptation to extreme temperatures, both low and high, or requiring less chemical consumption, can be great advantages in circumstances of drastic climate change. For example, dealing with a greater frost occurrence, higher average temperatures and/or water scarcity, drought, or efficient water use are some edaphoclimatic challenges best faced by perennial maize. Its better adaptation to high soil Al concentrations can lead to establishing plantations of perennial maize in places where annual maize would not be productive and, therefore, to soils with slightly more acidic pH than those supported by annual maize. This characteristic makes it an ideal crop as a planting alternative on soils where a change in soil management is desired. For example, the transformation of an abandoned forest crop to an agricultural one, since they tend to have a more acidic pH (Motavalli et al., 1995), or the suitability to do so on severely burned forest soils to restore them. Another difference between the cultivation of annual and perennial maize is that the latter begins its growth earlier than most annual maize varieties of temperate climates (Kantar et al., 2016), so these plants will have a greater capacity to capture water and nutrients since early growth occurs in early spring, which is when there is a greater probability of precipitation and also when nitrogen fertilization is carried out. Fertilization patterns should be adapted to this early development by establishing adequate fertilization schedules.

This, together with the perennials' ability to use water in advance and a more developed root system (that enhances the infiltration) will reduce run-off and, therefore, water erosion, reducing the transport of suspended solids and the nutrient load. As a result, an efficient crop management will be optimal by understanding the reproductive induction mechanisms of the perennial species, avoiding the spend of time and energy in vegetative growth at the expense of grain production. However, these adaptations must be experimentally tested on different cultivars at climatic zones necessitating the desirable traits for that growth environment, such as extreme conditions of pH, atmospheric temperature, soil temperature, water availability, as well as the presence of potentially toxic nutrients, to respond to existing gaps.

5.2. Perennial rye

5.2.1. Annual rye characteristics

There are many subspecies of rye, but the only one that is currently cultivated to obtain its grain for food, both human and animal, is *Secale cereale* (*S. cereale* L.). Rye (winter rye) grown in Europe is a winter cereal with low nutritional demands on the soil and is resistant to variations in temperature and humidity, both to frost and severe droughts (Miedaner et al., 2019). Its adaptability to extreme climatic conditions together with the improvements that can be achieved with perenniality make perennial rye a good option for farms located in temperate climatic zones, both ecologically and agronomically (Jaikumar et al., 2012). Rye is an outcrossing species and reproduced as synthetic cultivars. In the 70s, the first hybrid cultivars were introduced in Germany. These cultivars gave rise to higher production (15–20% higher than popular cultivars) and allowed achieving a selection to obtain a higher grain yield (Miedaner et al., 2019). Currently, the objectives to be achieved for the improvement of rye as a cereal consist mainly of increasing, in all branches of the plant, grain yield, by increasing the grain weight which is measured in thousand-kernel weight (TKW); increase resistance to diseases; decrease the protein content and increase the pentosan in the rye for baking; increase protein and decrease pentosan in the rye intended for food; and increase the dry biomass in rye intended for bio-methanol production (Miedaner et al., 2019).

5.2.2. Perennial rye state of the art

Perennial rye (*Secale cereale* L. × *S. montanum*) was obtained after crossing the annual variety *Secale cereale* L. (rye) with the close and wild perennial *Secale montanum* L. (perennial wild rye), whose chromosomes are homologous. Both species are diploid and cross-pollinated (Cox et al., 2002). Its perenniality allows it making better use of the moisture available in early spring, since the onset of its growth is early concerning the annual variety. It is a good competitor with weeds and produces a good regrowth, generating a high amount of biomass and being a good alternative for the production of both grass and forage (Acharya et al., 2004; Moyer et al., 2002). The perennial variety has a fibrous root system (Fig. 6) that improves soil structure, increases soil organic matter and protects the soil against erosion (Acharya et al., 2004). Although investments made in perennial varieties may not be profitable the first year of cultivation, since it would be an establishment period due to vernalization is required, once its root system is established, the perennial variety will grow earlier, more vigorously and will have the potential to have a higher yield in seed production terms (Jaikumar et al., 2012). Nevertheless, its productivity can be affected by competition with weeds. Moyer et al. (2002) have observed that, after the implantation period, perennial rye is tolerant to broadleaf herbicides used for weed control and these do not affect its biomass or its productivity.

Until the early 2000s, no perennial varieties had been used for large-scale grain production, mainly due to the difficulty of obtaining a fertile perennial generation. This was achieved with translocations that affect three of the seven pairs of chromosomes that come from the two species, the annual and the wild perennial, and *S. montanum* genes which govern perenniality (Cox et al., 2002), giving, as a result, a homozygous perennial and fertile variety. However, of all the possible ones, this is the rarest and its genomic content is the least compatible with good agronomic qualities. Currently, marker-assisted selection techniques are being used as helpful tools to select perennial varieties and improve their agronomic abilities (Pimentel et al., 2012). For example, experiments carried out by Weik et al. (2002), both in pure and mixed stands, showed that the productivity of rye was low. Therefore, it is important to improve the genotypes to increase crop yields for the cultivation of grain. Recently, perennial rye has been studied for grain production in Manitoba (Canada), although it has shown poor winter survival and high ergot occurrence, so these cultivars are not recommended for grain production in that area (Cattani, 2019). Although perennial rye is desired to become an alternative or supplement to the annual crop (Pimentel et al., 2012) to reduce global malnutrition, currently a cultivar that has a grain yield similar to that of the annual crop has not

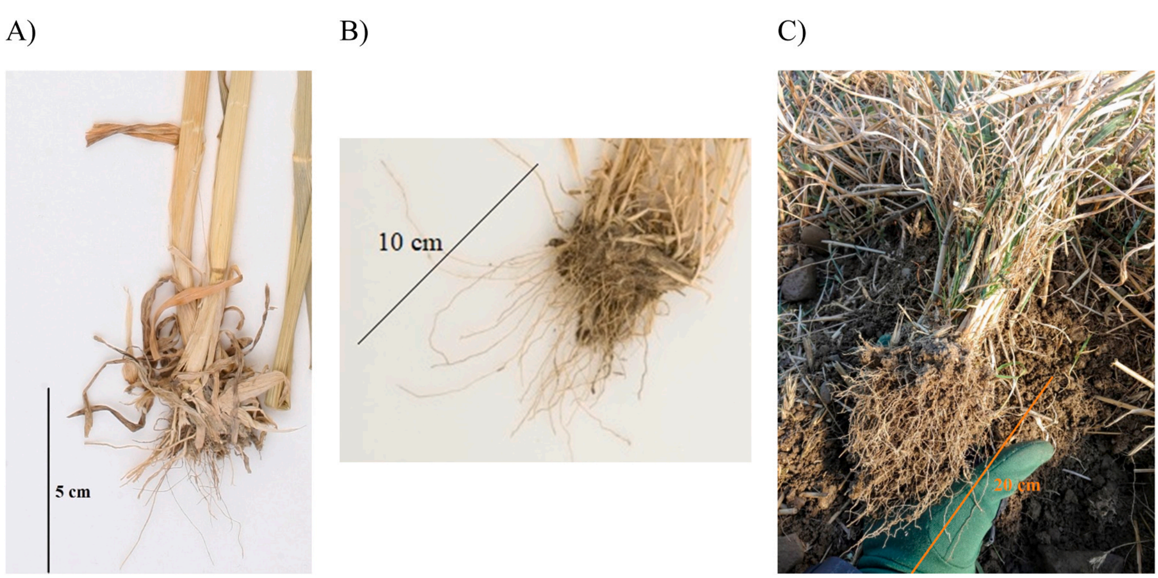


Fig. 6. Root system comparison among three varieties of rye: A) annual winter rye (*Secale cereale*), B) wild perennial rye (*Secale montanum*) and, C) perennial rye (*Secale cereale* L. × *S. montanum*).
Images modified from Wunderlin et al. (2021), Stutz (2020); and Law et al. (2018), respectively.

yet been found. The ACE-1 cultivar was developed in Canada to improve the production of silage for cattle (Acharya et al., 2004), is not susceptible to diseases or pests by insects and with good quality for ensiling. This was obtained by backcrossing its F1 generation with *Secale cereale* L. while selecting for perennial types (Reimann-Philipp, 1995).

5.2.3. Main conclusions regarding perennial rye

Perennial rye is a good alternative to forage wheat, its cost is lower, and it competes optimally with weeds (Bowman et al., 2007). From an environmental point of view, perennial rye has been recently compared with annual in experimental plots in Canada to examine their influence in CH_4 fluxes. The results obtained showed the perennial enhances soil methane sink due to changes in aeration-moisture balance as a consequence of increased root growth, for both grain and forage production (Kim et al., 2021). However, much remains to be done at the genetic level to improve perennial rye so that it can compete at the level of grain productivity with the annual variety.

5.3. Perennial sorghum

Perennial sorghum is another cereal that, along with rice and rye, can be hybridized with wild relatives to achieve perenniality (Cox et al., 2002; Kantar et al., 2016). Annual sorghum (*Sorghum bicolor*) is grown in different locations around the world, which differ significantly in edaphoclimatic conditions, where the purpose of sorghum plantations is the production of forage and biofuel (USA) or human and animal food (South Asia and Africa).

Sorghum produces a true stem and a basal stem or rhizome that extends both vertically and laterally. Sprouting of the rhizome is what determines the sorghum cycle and is influenced by temperature and soil humidity conditions. Plants sprouted from rhizomes are more vigorous and with higher productivity than those from the auxiliary buds of the true stems (Cox et al., 2018). However, wild perennials have a long-lasting rhizome which produces weaker plants, not optimal for a good agronomic performance of this cereal, while the rhizomes of the annual do not survive winter, degrading and eventually dying. Therefore, the challenge for a good optimization of perennial sorghum lies in combining the genes of the annual sorghum, which provide high-yielding rhizomes, and those of the perennial variety, which provide regrowth and survive winter, especially, cold winters in temperate climates to get a better adaptation to extreme climatic conditions. Sorghum is grown in hot, semi-arid areas, and tropical environments. It is a species drought-tolerant, although there are varieties that support or adapt better to more temperate or humid climates. Sorghum has a deep and diversified root system. Its cultivation is carried out in large fields in the form of ridges, so its presence helps to reduce soil erosion, especially in arid areas. Its optimal conditions for cultivation include temperatures between 20 °C and 35 °C, and rainfall between 150 and 950 mm (Peter et al., 2017). In addition, Peter et al. (2017) have established agro-ecologically suitable niches for its cultivation in Africa, showing that only about 25% of the land is optimal for the cultivation of sorghum, being, compared to maize and pigeon pea, the least suitable of the three. However, its cultivation is optimal in places where, for the other two, the conditions are not so ideal.

5.3.1. Sorghum perennial hybrids

Perenniality in sorghum has been achieved through the controlled hybridization of the annual sorghum with two wild varieties, i.e., *S. halepense* or *S. propinquum*. While *S. bicolor* and *S. propinquum* come from a common and diploid ancestor (2n = 20), *S. halepense* comes from the natural cross of *S. bicolor* and *S. propinquum* and a subsequent and spontaneous doubling of the number of chromosomes, resulting in a tetraploid species (4n = 40) (Cox et al., 2018). Recently, results found by Habyarimana et al. (2018) in northern Italy, where the perenniality was evaluated, suggest that satisfactory results are being achieved including higher yields.

Hybridization of annual sorghum with wild perennial sorghum has been easily achieved, since spontaneous crosses of both varieties arise in places where sorghum has been cultivated since ancient times (Cox et al., 2018). However, the optimization of perennial sorghum to increase the production of grain for human or animal consumption has not been achieved until recently. For example, Nabukalu and Cox (2016) have carried out a controlled experiment between crosses of the varieties *Sorghum bicolor* (L.) Moench × *S. halepense* (L.) Pers. to obtain perenniality, and, at the same time, an increase in grain production. However, grain yield was not correlated with the sorghum survival index, although grain size was negatively correlated with this parameter. For instance, Roozeboom et al. (2019) compared the grain yields and total biomass of various cereals, among which sorghum was studied: annual sorghum produced more biomass and higher grain productivity than the perennial one. Fortunately, some encouraging results were found by Habyarimana et al. (2018) where the perenniality, as well as the biomass and the yield of 97 lines of *Sorghum bicolor* (SB) × *S. halepense* (SH), were evaluated. The authors considered perennial sorghum as those plants whose rhizomes survived the winter and compared the results with data from historical lines of *Sorghum bicolor*. Hybrids resulting from crosses between SB × SH achieved perenniality, especially those carrying a higher genetic proportion of SH. In addition, some SB × SH lines were competitive in comparison to commercial productive hybrids of SB, both in terms of dry biomass production (38–45 t ha^{-1}) and grain productivity (5–11 t ha^{-1}). Additionally, they achieved satisfactory rates of perenniality (56–100%) and higher levels of fiber (61–69%). Recently, Nabukalu et al. (2021) have introduced perenniality from *S. halepense* into *S. bicolor*. They have detected traits that may regulate seed yield and support the development of high-yielding perennial grain sorghum varieties.

5.3.2. Main conclusions regarding sorghum perennials cultivation

The establishment of perennial sorghum cultivation can become an optimized reality at an agronomic level if the effort of breeders to obtain the appropriate genotypes and the study of agro-spatial climatic niches are combined: getting satisfactory and repeated results in terms of sorghum yield for grain, in addition, to develop it in different areas where sorghum cultivation is practiced traditionally will contribute to achieving satisfactorily this challenge. Other aspects that should be considered are the nutritional crop requirements and the edaphic conditions. They have not been studied yet in relation to the nutritional quality and productivity of perennial sorghum. Therefore, more research is still needed to go deeper into perennial sorghum at an agroecological level.

6. Future perspectives

Perennial grains are generating huge interest, given the potential for economic and ecological benefits associated with their cultivation. However, this interest has yet to translate into a shift towards perennial cropping systems. According to some studies, there is great interest among the farmers (Wayman et al., 2019), but many of them are concerned about issues such as seed price, increased pests, low grain yield or even yield loss over time. Moreover, for many of these perennial grain crops, a technology change is necessary (both for harvesting and for grain processing), and there must be an associated demand, as well as agricultural policies and legislation that take them into account (Duchene et al., 2019; Sanford et al., 2021). However, current technologies likely allow for great advances in the development of perennial grains, and that is why companies are becoming interested in perennial grains (such as General Mills), and even as the first perennial cultivars of some crops, such as Kernza, are being introduced in the market. It is important to transfer to society the benefits of consuming perennial grains to increase their acceptance.

It is of vital interest to carry out research in different climates and conditions to determine the viability and scope of these new products

(Hayes et al., 2018). Through these tests, it will be possible to determine the conditions that most favor the crops, or even adapt each species to specific geographical areas, allowing better use of the environment by reducing the number of inputs, tillage hours (and the associated soil loss), and reducing production costs. To this end, it is essential to establish breeding programs in different parts of the globe, with cultivars that include genetic material adapted to the environmental climatic conditions. It is also important to conduct comprehensive experiments under realistic depictions of future projected climate to consider possible climate-alterations affecting crop productivity and nutritional value (Leisner, 2020). Finally, it is crucial to take the needs of farmers into consideration (Wayman et al., 2019) looking for improving quality, yield over years, optimal practices, weed management, markets and economic assessment. Therefore, developing management guides that allow farmers establishing these crops (Lanker et al., 2020) and weaving a network that facilitates perennial crops to continue (with long-term experiments and with different processing and commercialization) would be a must to switch towards smart agriculture.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Glossary

Allohexaploid: Cells or species that have six copies of chromosomes from different species in their genome (Feldman and Levy, 2012). For example, wheat is a hexaploid species whose genome comes from three different species.

Endonuclease: Restriction enzyme that catalysis the DNA molecules breakdown (Berg et al., 2002).

Gibberellin: A hormone secreted by plants and some fungi that is responsible for regulating processes such as development and growth (Li et al., 2017).

Mutagenesis: The appearance of alterations (mutations) in the genetic material (Theodorakis, 2008).

Pentosan: A type of polysaccharide found in grains such as barley (Jankiewicz and Michniewicz, 1987).

Ratooning: It is the ability of the plant to regenerate new stems, i.e., regrow after being cut from the main plant, that is, after harvest following that of the main crop (Ziska et al., 2018).

Rhizome: The name by which the underground part of some plants that present buds is known (Chomicki, 2013).

Shattering (of the seed): Seed dispersal from a crop that occurs in some species with the ripening (Dar et al., 2018).

Stolon: An elongated, horizontal stem creeping along the ground and rooting at the nodes or the tip (University of Saskatchewan, 2021).

Totipotency: The ability of some cells to become any type of cell (Bhatia, 2015).