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PAST AND PROSPECTS OF FORAGE MAIZE BREEDING IN EUROPE. II. HISTORY, GERMPLASM EVOLUTION AND CORRELATIVE AGRONOMIC CHANGES

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ABSTRACT - Although maize was early recognized as an excellent forage plant soon after its introduction in Europe, during a long time it was only bred for grain traits. However, the first recommendations of maize varieties for specific forage use are probably those given in the French Vilmorin-Andrieux catalogues as early as the second mid of the 19th century. The 1940 Dutch variety list distinguished several types of maize varieties and was already recommending three varieties for silage use. Whereas US hybrids were introduced in Europe in the early 1950s, the significant extension of silage maize cropping began after the release of early flint x dent hybrids such as Inra258 (1958) and a little later Brillant DK202, Capella, LG11, and Blizzard G188 (between 1965 and 1975). The increase went on until 1990, with a decrease or stabilization following. The first generation of early European maize hybrids was mostly often based on crosses between flint Lacaune and dent Minnesota13 lines. The registration of Dea (1980) in France and a few years later Golda in Germany both illustrated tremendous changes in maize dent, and to a lesser extent flint, germplasm and marked the onset of a second era in European maize hybrid breeding. Iodent and BSSS origins were thus substituting for Minnesota13. Correlatively, the era of 1980s was also marked by significant improvement of hybrid earliness. The actual maize breeding is characterized by a significantly greater introgression of medium late germplasm into early dent and flint maize lines. The beginning of this last period may be dated by the registration of Banguy (1992). The average genetic improvement in whole plant yield was close to 0.10 t/ha.year during the period between 1958 and 1988, but reached 0.17 t/ha.year between 1986 and 2004. In early maize, highly significant improvements of stalk standability, stalk rot and lodging resistance have been achieved between 1950 and 2004 in Europe. Physiological changes associated to these improvements are at least delayed senescence of leaves and stems, higher grain filling rate, and higher stress tolerance. Conversely to agronomic value, a steady decline in the average cell wall digestibility of hybrids was observed since the 1950s, and maize of the next future have to give a better balance between agronomic and feeding value traits.

KEY WORDS: Maize; Corn; Silage; Germplasm; Yield; Earliness.

INTRODUCTION

Maize was introduced in Europe, first by Columbus in Spain (1494), and little later by Verrazano (1524) and Cartier (1534) in French Normandy (Rebourg *et al*., 2003). Within a generation, maize was grown in countries of central and southern Europe, along the coasts of Africa, and it reached China before the end of the 16th century, probably including the direct introduction of American germplasm via the Mediterranean sea. A secondary reintroduction of this germplasm from Turkey, Asia, and Greece, to western Europe could explain the "Turkish corn" name commonly given to maize in numerous European countries. The first use of maize in Europe was for human feeding, as it was traditionally in America. However, whereas the native Americans had no cattle, and thus little use for fodder crops, the value of forage maize for livestock was quickly

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recognized by Europeans since the periods of exploration and conquest of America, or after its introduction. BUNTING (1978) quoted an account of one America discovery expedition initially mentioned by WEATHERWAX (1954), in which it was stated that "the horses fattened and thrived … because of the large quantities of maize there, … the best fodder that grows". PARMENTIER (1791) observed that "cows eat maize forage greedily, and it makes them yield a lot of milk". During his travels in France, YOUNG (1792) categorized farms into "good" and "bad", according to the presence or absence of forage maize in cattle feeding. Conversely to a period of decline in maize grain production in Europe between 1850 and 1950, interest in maize was steadily maintained for cattle foddering, especially in France and Germany.

Maize was, for long time, mostly used as fresh green fodder for animal feeding during summer. Plant harvests began at pollination, leading to forage with very low dry-matter (DM) content, and went on during summer and early autumn up to small grass regrowth. Forage conservation by ensiling was first explored by Reihlen at Stuggart in the 1860s. Developments made by GOFFART (1875) and LECOUTEUX (1883) in France brought this technique to the attention of farmers in Europe, but also in the USA (BUNTING, 1978). However, silage maize development in Europe was low, mostly because early genotypes were not available or not used (WOODMAN and AMOS, 1924). At the end of 1940s and early in the 1950s, ensiling of maize was still not common in France (CAUDERON *et al.*, 1951) and in other European countries. Late or medium-late hybrids and high plant densities were most likely considered to be needed to maximize the green matter yield. The breaking point, and the switch towards higher DM, seemingly occurred first in 1950 in the Netherlands, and only maize varieties harvested between the milky and dough stage of grain maturity were gradually used in Europe.

Even if maize was thus recognized early as an excellent forage plant, its breeding was only focused on the improvements of grain traits over a long time. Before the advent of breeding theories and seed companies, farmers, sometimes unknowingly, chose the best ears when they produced or exchanged their own seeds. More recently, during the past 60 years, breeding efforts and financial inputs were also mostly devoted to grain maize. Breeding maize as a forage plant really began in Europe 25 years ago, first with introduction of whole plant experiments of grain maize hybrids, and progressively with a preferential use of some lines in forage or more often dual-purpose hybrids. Forage maize hybrids available in Europe (and elsewhere in the world) are still greatly based on grain maize germplasm, and genetic resources allowing further quality improvements of the maize crops have to be re-discovered. This review described the development of forage maize after the species was introduced in Europe, the history of early maize breeding in the 1950s, the joint evolution of germplasm and agronomic value from this date to nowadays. An overview on the evolution of forage maize feeding value during the 50 past years, and on prospects of further improvements based on the understanding of the grass cell wall biogenesis and biochemistry has been given in a recent complementary review (BARRIÈRE *et al.*, 2005).

FROM LANDRACES AND OPEN-POLLINATED VARIETIES TO THE EMERGENCE OF FORAGE MAIZE HYBRIDS

The first recommendations of maize varieties specifically devoted to forage use are probably those given in the VILMORIN-ANDRIEUX catalogues. In the catalogues of the period between 1870 and 1940, the open-pollinated (OP) varieties regularly recommended for cattle foddering were Maïs Jaune Gros "2 m height, very good for forage use", and Maïs Géant de Caragua or Dent de Cheval (horse tooth, probably synonymous with Blanc Dent de Cheval of SCHAD and VILLAX, 1951) "3 to 4 m height, the most yielding forage maize, fitting especially well for cattle foddering, with a white grain not ripening in northern France". The origin of this variety was debated between M. GOFFART and M. VILMORIN. It still remains unknown whether this OP variety (or landrace) came from USA (North Carolina, Georgia, and Maryland) with the name Caragua, or if it was first introduced from Nicaragua in Algeria, and later in France and Europe, the name Caragua being then a distortion of Nicaragua (WERNER, 1885). Improved King Philip was also proposed in the 1890s as "1.5 to 2 m height, very foddering, with a brown grain ripening easily in the north of Paris, with a similar yield as Maïs Jaune Gros, and about a similar earliness as Maïs Hâtif d'Auxonne". In England, the early variety Jaune Gros du Domaine used by WOODMAN and AMOS (1924, 1928) for forage experiments was introduced from France, and it was maintained in this country at least until the 1950s. It can be assumed that this Jaune Gros variety was the same one as the Maïs Jaune Gros proposed in the Vilmorin catalogues. Because names are identical after literal translation, Jaune Gros was probably the same variety as Large Yellow or Large Yellow Flint which were, with King Philip, three strains of New England 8-Rowed, generic term given to the Northern Flint-Flour race (GERDES *et al*., 1993). Corroborating this assumption, an OP variety named Large Eight-Row Yellow-Flint Corn, considered to be originally cropped in the state of New-York, was described in the review by WERNER (1885) of maize available in Germany. Typical Northern Flint type maize plants have 8 or 10 ear rows, but also numerous tillers, leading easily to the "foddering" recommendation. Several maize OP varieties were still offered in VILMORIN catalogues of the 1930s. However, the seed market became highly disrupted during the Second World War, all the more, as no maize seed organisation existed before the 1950s. The VILMORIN catalogues of the years 1949 and 1950 proposed only three late or medium-late maize landraces (Blanc des Landes, Dent de Cheval, and Roux des Landes, this last one seemingly never proposed before) without any comments on preferential grain or forage uses. Several landraces or OP varieties might have been lost during the war. US hybrids were introduced in Europe after the Second World War, with an earliness ranging from FAO 240 to FAO 500. In Vilmorin catalogues of 1949 and 1950, US maize hybrids were proposed without variety list, and with the note "ask us".

As soon as 1930, there was a maize variety list in the Netherlands with three OP varieties or landraces (Virgina Paardetand Mais, Gelber Badischer Landmais and Mais Jaune des Landes). In VILMORIN catalogues, Maïs Jaune Gros and Maïs Jaune des Landes were always considered as two different varieties. Ten years later, in 1940, several types of maize varieties were distinguished on the Dutch variety list (grain, bird seed, sweet, and silage maize), and three varieties (Vivo Paardetand Silomais, Blanc des Landes Mais, and Fleischmann's Goudtand silomais) were recommended for silage use. Based on VILMORIN catalogues and Dutch variety lists, and based on variety name, introduction of medium-dent germplasm could have occurred in Europe at least during the 19th century (paardetand also means horse tooth). US hybrids were introduced in the Netherlands since at least 1948. Wisconsin160, which could be presumed to be very early, was quoted by LACKAMP (1982) to have been experimented with at that time, but seemingly without further notable market share. In 1950, the first hybrid variety entering the Dutch variety list was Wisconsin240. Seeds of this hybrid were partly imported from the USA, but seeds were also produced in the Netherlands and marketed under the name of Amo. Whereas early breeding objectives were related to maize grain in the USA, France, and Germany, the main objective of Dutch maize breeders was the breeding of fodder maize, able to yield a large quantity of high-energy silage maize.

Before the Second World War, maize was of minor importance in the German agriculture and was cropped for cattle green foddering on probably less than 50,000 ha. However, it paved the way, especially in Bavaria, for the introduction of modern silage fodder preparation. Maize breeding was exclusively devoted to the improvement of several local and/or European OP varieties and landraces, mostly of flint type. The most well-known landraces and OP varieties at that time were Gelber Badischer Landmais, Dr. Delilles Neue Kreuzung, and Braunes Schindelmeiser. During the 1950s, when the first results with US hybrids (mainly from Wisconsin) grown in German less favourable climatic conditions were known, the interest in hybrid maize breeding activities was significantly stimulated. Several US hybrids, which produced up to 40% more than the best local varieties, were indeed a convincing incitement towards further investigations. On the initiative of the Max-Planck-Institute for Breeding Research at Voldagsen (later Köln-Vogelsang), the German Hybrid Maize Association was founded in the early 1950s and all breeders interested in maize became a member. The first maize hybrid breeding programs for different environmental conditions were set up, based on the local open-pollinated varieties (flint) and the available US hybrids and their parental components. Early forage maize hybrid breeding started simultaneously in the German Democratic Republic at the Institute for Plant Breeding in Bernburg/Saale. Breeding germplasm originated from the former Saatzucht Braune at Bernburg as well as from hybrids and/or their components from the neighbouring Eastern European countries.

The decade of 1950 was in European countries a transition period with simultaneous cropping of European landraces as well as US hybrids, with comparisons of the two types of germplasm in former forage experiments. Even if late germplasm was yet favored for maize forage and silage uses in the

1950s, the first report of experiments with a modern average DM equal to 30% was seemingly done by SCHAD and VILLAX as soon as 1951. Out of 18 medium-late varieties, harvested at the grain dough stage ("maturité cireuse du grain"), the "control" variety Grand Roux Basque yielded 8.8 t/ha (30% DM), which was outperformed by the variety was Blanc des Landes (10 t/ha, 26% DM). The higher yielding hybrid was Wisconsin595 (14.7 t/ha, 27.5 % DM), whereas the earlier hybrid Wisconsin416 (32% DM) yielded only 9.5 t/ha. Several other comparisons of hybrids were given in the same report, but with lower DM content in maize forage. Etoile de Normandie was compared with Wisconsin255 (of similar earliness) in an experiment with four harvest dates ranging from early August to early September. As average values of harvests, Wisconsin255 yielded 8.3 t/ha whereas Etoile de Normandie yielded 7.2 t/ha, both with an average DM content only equal to 18%. From experiments of DESROCHES (1955), hybrid yields did not often exceed yield of the Grand Roux Basque landrace, but hybrids proved to have a higher tolerance to lodging and stalk rotting and breaking. Moreover, leaves of OP varieties were dry at harvest, whereas leaves of hybrids were still green and probably illustrated a primitive stay-green.

In 1954, in France, 220,000 ha of maize were cropped for forage and silage uses, out of which 125,000 ha in the traditional grain maize growing area in the south-west, but at least 80,000 ha in area where grain maize cropping was not traditional (DESROCHES, 1955). Most of the seeds (about 2/3) used for cultivation were not certified seeds, but originated from grain maize produced on the farm, or from purchase of maize grains intended to be used for human or animal consumption. Experiments of offspring of hybrid varieties are thus often found in papers published at least between 1948 and 1955. In these ancient times, forage maize farm seed-production was considered as economically beneficial to farmers. The OP offspring of Wisconsin416, Wisconsin464 and Iowa4417 showed a decrease in DM yield only equal to 0.5 t/ha, while the DM content was only 0.4% lower. However, variable results with F2 seeds are found in literature of that time because seeds were not always inbred offspring, but a mix of offspring and crosses with other genotypes cropped in close locations. As a large part of maize was then even used as a green forage cut according to cattle needs during summer, DESROCHES (1955) soon considered that the greatest interest of maize was its use as silage for cattle foddering during winter, after harvest at the dough stage of the grain. Cropping of silage maize was recommended at 100,000 to 120,000 plants/ha, whereas the plant density recommended for green foddering was 200,000 plants/ha, or even higher.

In Spain, farmers also first planted the same maize OP varieties for cattle foddering than those that were used for grain, but at higher density. The first research in breeding (grain) maize hybrids adapted to Galicia was undertaken by Gallástegui (ORDÁS, 2003), in 1921, at the Misión Biológica de Galicia after training several years at the Universities of Hohenheim (Germany) and Harvard (USA), and at the Connecticut Agricultural Station (USA). Gallástegui began to self maize as early as 1921. First double crosses were planted in 1928, and were thus likely the first European hybrids. Since this year, double crosses were widely cultivated in Galicia and other areas of Spain. The two hybrids most widely grown were Pepita de Oro (yellow) and Reina Blanca (white). The first was obtained by the cross of Longfellow (L) inbreds to Gold Nugget inbreds (GN) with the original scheme (L × GN) × (L × GN). The white hybrid was made with the formula (Sanford White × Arcade) × (Henderson's Large White × H bl.). Sanford White and Henderson's Large White were flint US OP varieties, Arcade was obtained from a local landrace and H bl. was an inbred obtained by conversion to white of a strain of Gold Nugget. Whereas Gallástegui also carried out research with dent maize, only used flint hybrids were released due to the custom of the farmers in the region that only cultivated flint types. This important activity was stopped in 1939 because of the closing, after the end of the Spanish Civil War, of the farmer syndicate that Gallástegui had established for hybrid spreading. The early inbred line EP1 was also developed by Gallástegui from a Basque Country landrace, but it was not used in Spanish hybrids. EP1 found its way in Europe when it was sent for the FAO cooperative works sponsored by FAO in the 50's. Gallastegui's hybrids were too late for many areas of Galicia except the southern part of the region. ESCAURIAZA (1935) thus complains that both Pepita de Oro and Reina Blanca have serious problems to be grown successfully in the North of Galicia. In the 1940s, two other breeding programs were started in Spain, but both of them were aimed at grain maize. However, the forage value of the hybrids included in the official (grain) list was investigated by different extension offices of the Ministry of Agriculture or regional institutions over the years.

Maize is also one of the most important crops in Italian agriculture. The plant was introduced into the Italian cultivation system approximately four centuries ago and grown mainly for human consumption. Since the end of the second World War, the Italian agricultural scene has changed and the subsistence mixed farming unit, operating on a more or less closed circuit system, is now transformed into a monoculture "green factory". Main factors contributing to the enhancement of maize yields, including silage production in the Po Valley which is the core area of Italian maize production, were the use of medium-late hybrids (FAO 600-700), with high levels of nitrogen fertilization, irrigation and/or the presence, frequently, of a higher water levels in the soil, and the constant introduction of better performing varieties. Although international breeding companies have played a substantial role in proposing to the growers their most recent hybrid varieties, the Maize Station of the Istituto Sperimentale per la Cerealicoltura of Bergamo has developed an active maize breeding project in the last three decades. The primary objectives of this project have been to develop inbred lines for use in hybrids to be grown in the Po Valley, and to conduct research to evaluate characteristics of commercial and experimental hybrids for both grain and silage productions.

During the early stages of development, and especially in the cold conditions of northern Europe, maize is particularly susceptible to weed competition because of its slow growth. Simultaneously to the availability on European market of the first hybrids more tolerant to low temperature was the introduction of triazine herbicides (Atrazine and Simazine), to which maize is outstandingly resistant. Weed control allowed simultaneously the use of lower plant densities in forage maize cropping, fitting well with the potential of newly developed hybrids and allowing higher DM content at silage harvest. Moreover, in the early 1950s, grain and forage maize had to be hand-harvested, and according to Lackamp (1982) no silage harvesters were available on Dutch (and likely other European country) farms in that time. The "wheeled choppers" were introduced by Danish farmers, seemingly in second half of 1950s or early 1960s (Lackamp, 1982). Besides genetic improvements, maize indeed turned into an inescapable fodder crop due to the possibilities offered by chemical weed control, a complete mechanization of plant cropping from sowing to harvest, and an easy and reliable conservation method. A very efficient management of high quality seed production was also set up at that time through farmer associations and cooperatives.

GERMPLASM EVOLUTION IN FORAGE MAIZE. I) FROM US HYBRIDS TO LG11

The review of hybrids cropped between 1950 and today highlighted first a former period corresponding to the introduction of hybrids during the 1950s decade, with the progressive cropping extinct of older landraces (even if few ones were still available for years), followed by the conquest of European countries by European bred flint x dent hybrids during the 1960s and 1970s decades. All US hybrids available for European farmers in the early 1950s for cropping in northern areas were indeed dent x dent crosses, except Wisconsin240 whose male parental lines are related to northern US (W15) and Canadian (W85) flint germplasm (the pedigree of Wisconsin160 was not still found again).

The first early flint x dent hybrid developed in Europe was most likely Goudster obtained in the Netherlands by Van den Eijnden (Dolstra and de Jong, 1984), and it led to a first increase of maize area in northern Europe in the beginning of the 1950s (Bunting, 1978). Goudster was included in the Dutch variety list in 1952 as a hybrid between "little inbred families" bred from the German flint Chiemgauer and from Noorlander and Baanbeker, selections previously made in the US dent landrace Early Butler (Dolstra and de Jong, 1984). Early Butler, also called King of the Earliest, originated from Grand Valley in Pennsylvania (Labate *et al.*, 2003; Belsito, 2004). According to the present rules, Goudster as it was described in 1952 should be considered as a top-cross variety rather than a hybrid, but in the 1960 variety list, Goudster was still present and called a double cross hybrid. The maize breeding community in the 1950s had seemingly a broader opinion than now about what was a hybrid and a variety. In the 1950s, there were several other Dutch hybrids available on the official Dutch variety list. The first Dutch hybrids after Goudster were hybrids like CB42, CB32, CIV2 (or Prior), being all hybrids from the two farmer-owned breeding companies in the Netherlands, Cebeco and CIV (now Zelder). According to Lackamp (1982), Prior was a cross between the hybrid WH x WH as female and Baanbeker as pollinator. Another nucleus of hybrid breeding the Netherlands was in the province of Zeeland by a Foundation for maize breeding (Caldera hybrids, Capella, for instance), whose hybrids were commercialized by Van der Have (now Advanta). In 1955, only two OP varieties were still present on the Dutch variety list (Vroege Gele Ronde C.B. and Kuma), but there were already eight hybrid varieties (Matador, Goudster, Prior or CIV2, Wisconsin240, Foliant, KE3, Nodak301, Pioneer396, with the three last registered in 1955). Ninety percent of the acreage was already sown with hybrid varieties at that time. In 1965, six forage maize varieties were registered on the Dutch variety list.

In 1955, only 14 genotypes were registered in France, including the two French flint landraces Etoile de Normandie (early) and Millette de Finham (late), and 12 dent double-hybrids bred in the USA including the early or medium early Wisconsin240, Wisconsin255, Wisconsin355, United2, United22, United24, and Minhybrid706 (JUSSIAUX, 1955). The breaking events were improvements in tolerance to low spring temperature, in silking and ripening earliness, associated with the emergence of dent x European flint hybrids. INRA200, which was in 1957 the first hybrid developed and registered in France, was thus a cross between WH x WJ and F7 x F2. WH x WJ was the male of Wisconsin255, both lines bred in Wisconsin25 which derived from a cross between Minnesota13 and an early yellow dent of Michigan OP variety. The early flint lines F7 and F2 were selfed in the French Lacaune landrace (PROMAÏS, 1999). INRA258, registered one year later in 1958, was an original hybrid from all other hybrids developed in this era. Its male parent was not F7 x F2 but F7 x EP1, and its female dent parent (F115 x W33) yet included a dent line bred in France (F115, selfed in an open-pollination of Ia153), whereas most female dent parental hybrids were in that time crosses between US early dent lines. Another probable trait typical of this period was the non-definite choice of flint resources. F10 x Fc22 (selfed in French landraces Etoile de Normandie and Chavannes, respectively) was the female hybrid of INRA244, registered in 1957, with a male WD x W9 (that was the female of Wisconsin240 and Wisconsin255). Similarly, F65 x F66 (selfed in French landraces Bareilles and Sost, respectively) was used in INRA190 registered in 1967. These two hybrids and their flint female lines have seemingly no (great) commercial success. Sprint180, registered in 1974 by Limagrain had a female F65 x F74 (F74 was selfed in the Pyrenean landrace Aleu). Another genetic switch in the period of 1950-1979 was the registration of LG11 (1970, in France). This hybrid was one of the first three-way cross, and its male US dent line (W401) was significantly later than its parental female hybrid (F7 x F2). This hybrid also had a greater tolerance to higher densities (90 to 105,000 plants/ha), and was highly suitable for silage use. Just later after the release of LG11, in 1972, INRA240 [(F107 x F113) x (F7 x F2)] was registered, the first early INRA hybrid with all parental lines bred in France.

The first German hybrid maize varieties were registered and released in 1960 by the Federal Variety Office and could be produced and grown as of then. These first hybrids were top-cross hybrids which had resulted from US single crosses (mostly WH x WJ or WD x W9) as female, and flint populations (different local OP varieties) as male components, which was a similar hybrid scheme as it was simultaneously developed in the Netherlands. The breeding program of the Max-Planck-Institute developed the first German double cross hybrid based on four new independent early maturing inbred lines. This early maturing hybrid was registered by the Federal Variety Office in 1965 after 5 years of official registration trials under the name of Velox. In the German Democratic Republic, maize breeding had a similar development and led to the inscription of the first top-cross hybrid with a dent single cross coming from the Ukraine (probably of US origin) as female, and a local flint population as male component. These first hybrids out-yielded the best open-pollinated varieties available, by up to 40% in grain production. Moreover, they were significantly more resistant to lodging, trait of great interest in silage maize cropping.

During the period in the 1970s, most of the spectacular increases in the area of forage maize in Western Europe, that began from 1965, also occurred (BUNTING, 1978). This increase went on until 1990 with a decrease or stabilization after this time in most European countries (Table 1). LG11, INRA258, Blizzard G188, Brillant DK202 and Capella were among the most popular maize early hybrids used for silage in Europe during the period of 1970-1980 (Table 2). Average DM yield was close to 12 t/ha DM, and ranged from 10 to 15 t/ha, with a DM content ranging from 20 to 30%. The average DM content at the harvest increased in the Netherlands from 23% in 1970 to 27.5% as soon as in 1975.

TABLE 1 - *Areas of forage maize crops in various European countries (10^3 ha, from a large compilation of data; - are data not found again to date; maize areas before 1970 gathered green foddering and silage uses).*

	1955	1960	1965	1970	1975	1980	1985	1990	1995	2000	2004
Austria	–	–	–	35	80	–	–	–	–	–	–
Belgium	–	–	5	18	66	95	126	133	157	185	171
France	220	–	360	400	870	1170	1405	1647	1475	1397	1451
Denmark	–	–	–	–	2	8	10	16	35	57	117
Germany	90	480	350	520	780	1054	1282	1284	1252	1154	1289
Italy	–	–	–	–	–	–	–	–	–	–	300
Spain	–	–	–	–	–	–	107	113	104	82	90
Switzerland	3	–	5	11	22	–	–	–	–	–	–
The Netherlands	–	0.6	3	5	78	140	177	200	245	240	240
United Kingdom	–	–	1	2	25	–	–	–	–	–	–

TABLE 2 - *Most popular early maize hybrids used for silage production in northern Europe in two different eras (Data between 1965 and 1980 according to* Cottyn *et al.*, 1976; de Boer, 1976; Kilkenny, 1976; Laber, 1976; Lelong, 1976; Molle, 1976; Schneeberger, 1976; Zimmer and Zscheisscher, 1976; Bunting, 1978, *and the different contributors, in decreasing order of cropped areas. Preliminary data between 1980 and 1990 from the different contributors. Capella and Caldera535, and As and Keo, are synonymous, respectively).*

	Most popular maize early hybrids used for silage in the	
	1965-1980	1980-1990
Austria	Inra258, LG11, Austria290	Dea
Belgium	LG7, LG11, CP170, Anjou210, Inra258, Anjou196, But234, Fronica	LG2080, Mammouth
Denmark	Anjou210, LG11, Fronica, LG7, Capella	
France	LG11, Inra258, Inra240, LG7, Blizzard G188, Adour250, Dekalb216	Antarès, Apache, Aviso, Dea, DK250, Mona, Fanion, Keo
Germany	Blizzard G188, Brillant DK202, Forla, CP170 and Inra200	As, DK250, Golda, Helix, Mona
Italy	DekalbXL73, Regina, Peruviano, First	Lorena, Ranger, Fedro
Switzerland	Orla230, Orla270, LG11	
The Netherlands	LG11, Capella, Leopard	Brutus, LG2080, Splenda
United Kingdom	LG11, DK202, Caldera535	LG2080

Starch content was then mentioned as a quality related standard trait. In 1976, in Germany, one landrace (Gelber Badisher Landmais) and two topcross varieties (Pamo and Perdux) were still available among 40 varieties on the official list. The first very early hybrid was also registered at that time in Germany (Edo, 1974, three-way hybrid by KWS), with a very high ear/whole plant ratio, thus resembling a grain maize more than a forage maize.

During the period of 1957-1979, flint lines were mainly related to Lacaune F2 and F7 lines and to the Spanish line EP1. Gelder Badisher Landmais germplasm was afterwards introduced and played an important role in the development of early flint lines. To a lesser extent, Swiss line CH10 (Linth) and German line Du101 (Umkirch) were also used in second cycle line breeding. Most of these lines had a medium (F2) or high (F7) cell wall digestibility. During the period 1958 - 1975, most of important hybrids used for silage in France, Germany, and probably even in the Netherlands, had F7 x F2 as one parental hybrid. Based on 16 hybrids significantly used for silage in Europe during the period of registration between 1958 and 1972, 13 hybrids had F7 x F2, two had F2, and one had F7 x EP1 as flint parent. However, the end of the 1970s also corresponded to the progressive disappearance of the F7 line in hybrids, mostly due its susceptibility to stalk rotting. This first change in flint germplasm probably dated a beginning in the average decrease of cell wall digestibility in early hybrids. The F7 line was however used in second and further cycles of breeding, but seemingly few important recent hybrids have a flint line more or less related to F7. Early dent lines involved in hybrids of this period were introduced mainly from the University of Wisconsin, with a large use of W401, W182E (medium cell wall digestibility) and W117 (high cell wall digestibility), but also from Canadian universities with a significant importance of Cm7, Co109, Co120, Co128, Co125 (low cell wall digestibility in Co125). Origins of W401 and Co125 are still unknown, but Co125 likely comprised a Northern Flint group. W117 and W182E are both second cycle lines related to Minnesota13. Co109 originates from Early Butler, and Cm7 includes Northern Flint germplasm at least with its W85 parentage. Co120 and Co158 were selfed in Dekalb46, double hybrid released in the USA as early as in 1947, with two heterotic lines related to Minnesota13, one to Krug yellow dent, and one to Colonel Campbell (North Dakota landrace possibly related to a Northern Flint origin). Dent lines bred in Europe progressively replaced US bred lines in important hybrids of this generation, such as F113 (dent male in INRA240 and Fronica) bred by INRA in the US hybrid Spooner [probably (W37A x W37) x (W47 x EK43)] with at least three lines likely related to Minnesota13. Similarly, F107 selfed in F115 x W33 was involved in INRA230 and INRA240, both registered in 1972. Brutus, bred by Verneuil, which has been an important hybrid of good cell wall digestibility in the Netherlands, had a male dent line related to W401 (and F7 x F2 as female). During the period between 1958 and 1980, most of the important hybrids also had a dent parent related to Minnesota13, or in more northern area or in more earliest hybrids a flint-dent parent related to Northern Flint and Minnesota13. Several strains of Minnesota13 were later proved to be a dent origin of high cell wall digestibility. According to TROYER (1999), breeding of Minnesota13 began by the purchase of a common yellow dent corn cultivar in 1893 in St Paul that was further bred at the University of Minnesota. Quoting HAYS (1904), TROYER (1999) reported that Minnesota13 also moved grain corn growing northward 80 km in the USA in a decade (1895-1904). This could contribute towards explaining the important use of Minnesota13 progenies in early European maize breeding. From a study of 57 accessions representing maize US germplasm, based on 20 SSR loci, LABATE *et al.* (2003) showed that the most strongly supported relationships were the distinct clustering of flint accessions (Northern Flint, Longfellow, Falconer) away from all other accessions. Even if no higher-order groups were found within the non-flint germplasm, Lancaster was the closest relative of flint origins, followed closely by a cluster gathering Minnesota13 and Osterland.

Early investigations in breeding maize for forage use were also developed in southern Europe with late germplasm. In the 1950s, a new program started in Spain at the Misión Biológica de Galicia with the very original objective of developing hybrids with a simultaneous double use for both grain and forage. With these new varieties, it would be possible to ensile the stover after the ears were collected. Farmers could thus produce high quality silage due to a high content of sugar in the stalk. Whereas three double crosses with these characteristics were released, only one of them, D.M.B.5-8 [(EP5 × EP2) × (EP3 × EP4)] was extensively cropped. EP5 was a selection of Illinois R86, EP2 originated from a dent landrace named Maíz Alto de León and EP3 and EP4 had been developed from Longfellow. The formula was then based on the dent x flint heterotic pattern, with all the material being from the US, as Maíz Alto de León was probably a selection of Lancaster. This hybrid was the most widely cropped for many years in the FAO300 maturity group, but farmers did not use this hybrid as their breeders have intended it. D.M.B.5-8 was grown either for grain or for silage, but not for both. In this period, among hybrids frequently used for forage were D.M.B. 5-8 (and later INRA260 and Dea).

In Spain, the first official list of maize varieties of maize was established later (1968), and it was a grain maize list. However, at the end of the list, several varieties were given as being exclusively for forage use (Agrasa n° 1, Agrasa n° 2, Funk's, Hybrid White, Mexican June, Pioneer P500, Pioneer P510, Pioneer P580, Prodes, Semillas Agrícolas and Tuxpan). Most of these genotypes were hybrids, but some of them were obviously OP varieties (Mexican June, Tuxpan). Others were only described by the name of the seed companies (Agrasa, Funk's, Prodes, Semillas Agrícolas). In Italy, hybrids mostly cropped for forage use in the 1960s were Cervino, Dekalb Silage, Mielmais, Cise 780, Funk's G33. These (medium) late genotypes are likely also genetic resources of interest in early forage maize breeding.

GERMPLASM EVOLUTION IN FORAGE MAIZE. II) DEA AND THE IODENT REVOLUTION

The registration of Dea (1980) in France and Golda (1984) in Germany both illustrated tremendous changes in maize dent, and to a lesser extent flint, germplasm, and marked the beginning of a second era in European maize hybrid breeding. These two hybrids also highlighted the economic feasibility of single-way hybrid seed production, despite the important differences in silking date of parental lines, as well as single-way hybrids allowed exploiting heterosis maximally.

Golda is the model of hybrids having an early B14 related line (A632, Cm105, Cm174, …) as female and Co255, or a Co255 type (Co244, Co245), line as a male (Co255 was selfed in INRA258). Besides Golda, Mammouth, Splenda and Carlos became important forage hybrids, covering a large part of the silage market. Cell wall digestibility of this type of hybrids was often low, mostly because of the low cell wall digestibility of the B14 related parent. However, Golda type hybrids were mostly developed in continental areas (Germany, the Netherlands), whereas Dea type hybrids had a large market share in all European countries.

The dent parental line of Dea is related to the Iodent germplasm that was seemingly not used in European dent lines breeding before the release of Dea. Iodent germplasm became the foundation of all early hybrids and the basis of further early maize improvements in Europe. Iodent or Iodent Reid (Iowa experiment station Reid Yellow dent) originated from an ear-to-row breeding for earliness started in 1909 in Reid Yellow dent (TROYER, 1999). Reid Yellow dent cultivar was carried from the Reid farm (Illinois) to the Iowa State University in 1902, and several modified Reid strains are deeply involved in modern maize germplasm. The basal Iodent Reid line I205 was released in 1937, giving hybrids with erect plants, high yields, tolerance to several diseases and to European corn borer, buts low dry-down of ears (TROYER, 1999). Modern early Iodent lines, obtained after introgression of a long ear strain germplasm (12.5%), and three cycles of recurrent line breeding, were the result of a work started in Minnesota in 1958, aiming to improve both silking date and drying rate. The basis of the developed Rinke method were the two faster drying late Iodent lines, and three early silking Iodent Reid lines including B164 developed by Pioneer. The three early silking lines were also chosen because "they contributed excellent yield and very good stalk strength to their hybrids" (TROYER, 1999). The fourth and fifth cycle of breeding aimed to improve earliness, grain yield, diseases and pest resistance, with most emphasis in the fifth cycle on stay-green and ear development (TROYER, 1999). Breeding Iodent lines for grain production, stalk strength and pest resistance has certainly contributed towards their decline in cell wall digestibility. The most famous line from the fifth cycle was Pio165 (called Idt4A in TROYER, 1999). During the 1970s, the European Pioneer Hi-Bred breeding station based at Selommes (near Blois, France) evaluated the US bred Iodent lines in crosses with European early flint testers, and particularly with line F2. All these Iodent lines expressed a very high level of combining ability, giving several registered hybrids. The most important one was Dea, a single cross between Pio165 and F2. Dea was registered in France in 1980, based on its outstanding grain yield performances in the medium-early maturity group. Dea spread-out rapidly during the 1980s throughout northern Europe (France, Germany, Austria, Switzerland, Belgium, the Netherlands) taking more than 50% of the grain and forage markets. Sales of Dea remained significant until the mid 1990s. All the Iodent lines were developed in the northern Corn Belt for their high general combining ability (GCA) with BSSS and Lancaster inbred lines as testers. Information specifying surely the tester that was used during the breeding of F2 is seemingly lost. However, according to old INRA nursery notebooks, F2 was probably bred with a WD x W9 tester, related to Minnesota13, in experiments with Wisconsin255 as control hybrid. The excellent heterotic pattern of F2 against Iodent germplasm was therefore partly fortuitous, but both F2 and Pio165 had an exceptionally high GCA. During the decade of the 1980s, practically all European maize breeding companies developed their own "Dea type" Iodent hybrid, mostly using sister lines of Pio165. Out of these hybrids, DK250 (Boss in Germany) which was a little earlier than Dea had, with LG22.50 (Argos in Germany), and to a lesser extent Adonis and Colt, an important share of the silage markets in France and Germany. However, during this period, original genetic basis were also tentatively developed. Helga, first registered in Canada and registered in France in 1989, was a cross between Canadian bred lines, but appeared little adapted to European conditions. Nowadays, Iodent sources generated several derivatives and still are an important germplasm base for breeding the early to mid early maize hybrids.

The 1980s era was also marked by significant improvement of hybrid earliness. In the Netherlands, an important breakthrough in the period of the mid-1980s was the registration of LG2080 that was much earlier than all available varieties, with only a slightly lower yield. A new standard of "very early" maize was specially created for this new hybrid, giving a great impulse to the development of very early forage maize genotypes. In 1994, 15 very early varieties were then available, out of which 10 were newly registered. Comparisons of new hybrids to Brutus illustrated the earliness improvement of germplasm during the period between 1980 and 1990. Brutus was registered in 1980 in the group of early varieties and was one of the earliest varieties of the Dutch variety list. In 1994, Brutus was in the mid-early group and was one of the latest hybrids of the list. Similarly, in France, whole plant experiments with measurements of yield, DM content and lodging resistance have been done for maize registration with forage specification since 1986. Two earliness groups S1 and S2 were then specified. S1 gathered earliest hybrids (Brulouis and Leader Pau207 as control hybrids in 1986, Apache and Lixis LG2221 in 1992), and S2 contains less early hybrids (Dea and Baron as control hybrids in 1986, Lg2250 and Dea in 1992). In 1993, a third earliness group S0 was specified, accompanying the development of very early hybrids with high biomass yield (very early S0 with Lg2080 and Apache, early S1 with DK250 and Sem270, and medium-early S2 with LG2250 and Dea as controls, respectively). Increase of the forage maize area in Denmark also indicated the efficiency of breeding for early high yielding maize hybrids. In 1980, less than 10,000 ha of silage maize were cropped, but there were more than 130,000 ha of fodder beet, while, in 2003, only 10,000 ha of fodder beet were still present, but silage maize has increased up to nearly 120,000 ha (with hybrids such as Tassilo, Banguy, and, to a lesser extent, Vernal and LG3214). The significant improvement of hybrid earliness is related to a modified plant physiology, with plants later silking and having correlatively more leaves and a higher leaf area index, but with faster grain filling and grain drying. This genetic improvement was most likely achieved through breeding dent lines in crosses between Iodent and other "older" early dent germplasm. Moreover, significant improvements in tolerance to spring low temperature were found with lines more closely related to German flint, Northern Flint, and Canadian flint, than to Lacaune flint, and possibly from introgression of germplasm of tropical highlands or early flint from south Argentina and Chile as well. Among innovative hybrids for both whole plant earliness and yield were registered Aviso (1986) with a dent line not related to Iodent, Fanion (1991) with a flint line including only 12.5% of F2, and a dent line related to Iodent, Wisconsin and Ontario germplasm, Magister (1992) with a flint line not related to F2, but related to F7, EP1 and Bade Yellow types. Among early or very early innovative hybrids, four varieties, Apache (1987), Helix (1993), Antares (1993), and Scarlet (1994), with a cell wall digestibility similar to that of LG11, were registered during this period. Antares had a flint line related to F7, and Scarlet had a flint line related to F2, Ep1, and Canadian germplasm.

GERMPLASM EVOLUTION IN FORAGE MAIZE. III) THE END OF TRADITIONAL BREEDING SCHEMES

The actual maize breeding period is characterized by an important genetic improvement of hybrid for whole plant yield, a broadening of the genetic base of early maize breeding through introgression of medium late germplasm, and a continual decline in the average cell wall digestibility despite a greater specialization of hybrids in forage and grain types. The onset of this period may be dated by the registration of Banguy (1992). Striking events illustrating the genetic evolution occurred since Banguy registration were the registration of Anjou285 (1994), and few years later, the registration of Benicia (1997), Eurostar and Nexxos (2000). Banguy is the first important early hybrid whose heterotic pattern was no longer based on a typical Iodent x F2 scheme. Its female line included at least BSSS and Iodent germplasm, and its flint male line was related to F7 and F2. Anjou285, which had an important market share in France, differed from Banguy with a flint parent only little related to F2 or Lacaune landrace. Out of hybrids of this generation, Benicia (1997) is a high whole plant yielding hybrid with a predominantly dent original genetic background, that is mostly used in Germany. Anjou258 (1996), with the same dent female as Banguy and an original flint parental line resulting from intercrossing Western European, Eastern European and Canadian flint origins, illustrated modern hybrids with both high yield and earliness, and a cell wall digestibility equal to that of Dea. Similarly, in the Netherlands, the very early hybrid Rosalie (2002) is the most important on this market due to its good agronomic and energy values, the later related to both a convenient starch content and good cell wall digestibility. Eurostar and Nexxos illustrated the most common new pattern of hybrids, with their flint parental lines introgressed of dent germplasm. Besides Lancaster, BSSS or Iodent germplasm, exotic or late flint resources are also being used to improve early flint lines. The period of the 1990s is thus correlatively characterized by the disappearance of F2 as male line of early hybrids. Whereas about 250,000 and 500,000 MGV (10^3 kernels) of line F2 were annually sold by Frasema from 1980 to 1984 and from 1985 to 1990, respectively, less than 100,000 MGV and less than 30,000 MGV were sold in 1995 and 1997, respectively. Early dent lines, or dent lines, used in early modern type hybrids are bred in crosses of Iodent with Reid, BSSS or Lancaster germplasms, and gave hybrids significantly out-yielding Dea type hybrids. These hybrids are late flowering, but have fast grain filling and drying, an important stay-green, and most often a stiff stalk and a low cell wall digestibility. Even if Iodent germplasm, and to a lesser extent F2 germplasm, remain two inescapable bases in modern early maize breeding, elite genetic resources used in early maize breeding broaden beyond usual limits of earliness groups. Moreover, the usual and long time considered intangible flint x dent heterotic pattern, without crosses between flint and dent resources, and without the significant use of crosses between early dent and medium late or late germplasm families (BSSS, Iodent, Lancaster, …) became outdated in early European maize hybrid breeding. Especially, selfing in early or medium late registered hybrids was for a long time considered as an impasse in maize breeding because of breaking off of further heterotic patterns. It appeared conversely that innovating lines were obtained based on such processes, questioning both the possibility of fixing a part of heterosis, and the greater possibilities, than those usually considered for breeders, in shaping combining ability groups.

Contrarily to this use of a greater number of maize families in breeding early maize, a lower allelic diversity was described in hybrids (or their parental lines) more recently registered in France. Based on 20 markers, 71% of lines were unique genotypes in a set of 219 parental lines of early maize hybrids registered in France in 1990, whereas only 31% were unique genotypes in a set of 373 parental lines of hybrids registered in 2004 (Lallemand, 2004). Similarly, Le Clerc *et al.* (2005) showed that hybrid diversity, based on 51 SSR markers and 133 hybrids, has been reduced by about 10% in maize cultivars bred after 1985, compared to cultivars bred before 1976. Since novel variation was introduced, the decrease of allelic diversity in more recent hybrids could thus result from the plant improvement. Markers linked to unfavorable alleles were eliminated during the breeding processes. The use of similar genetic resources (Iodent, ISSS, Lancaster, Lacaune, …) is also expected to result in the independent choice of the same favorable and rare alleles. However, these results could be biased by the simultaneous decreased number of companies involved in maize breeding (35 in 1985 vs 15 in 2004), and by the greater number of hybrids registered by each company. Numerous hybrids are consequently related and based on common parents or sister lines. The study of pedigree backgrounds of 68 Pioneer grain maize hybrids widely grown from 1930 to 1999 showed that they collectively traced to at least 61 founders and 22 landraces, with additional contributions from other genetic resources (Smith *et al.*, 2004). New founders contribution mostly occurred in each era of breeding, but most especially in the 1940s (35%), 1960s (36%), and 1980s (20%). Pedigree relatedness among hybrids released during the same decades increased during the 1970s and the 1980s, and has then remained stable during the 1990s. A reduction of genetic diversity of maize elite resources in more recent hybrids seems in fact very questionable, including in European early hybrids. Whereas the number of independent elite resources in each company had probably decreased, mostly due to the level of achievement of each elite germplasm was greatly improved, new resources were regularly introduced such as medium late US dent, exotic, Canadian, and central Europe flint germplasms in early forage maize breeding.

PROSPECTS FOR NEW IMPROVEMENTS OF AGRONOMIC TRAITS IN FORAGE MAIZE

Even if breeding was partly based on grain traits, impressive improvements of forage maize whole plant yield, earliness and stalk standability were observed during the past 50 years. During the period between 1950 and 1980, the correlative improvement in whole plant yield of early hybrids was close to 0.07 t/ha.year (BARRIÈRE *et al.*, 1987). More than half of this yield gain was observed within the first ten years when hybrids such as INRA258 replaced hybrids such as Wisconsin240. LUCIANI (2004), studying all forage hybrids registered in France between 1991 and 2003, found an average yield improvement close to 0.18 t/ha.year, occurring earlier in very early and early hybrids than in medium early ones. A similar trend was also found from average values of the best hybrids in each maturity group (Table 3). In the Netherlands, when comparing with the most important variety at the beginning of the 1970s (Capella), the DM yield was increased by 20% during the further 30 years of plant breeding and simultaneously the varieties were earlier by an average value close to 20%. In Germany, the genetic progress is impressively illustrated by the increase of grain mean yields of the check varieties in the official registration trials organised by the Federal Variety Office, ranging from 0.14 to 0.17 t/ha according to earliness group. Simultaneously, highly significant improvements in early grain maize stalk standability and stalk rot resistance have been achieved between 1950 and 1980 in Europe (DERIEUX *et al.*, 1987). Lodging resistance was similarly greatly improved in forage maize. From observed values in registration control hybrids during the period between 1986 and 2001, average plant lodging decreased from a little more than 10% to a little less than 5% (LUCIANI, 2004). The improvements in stalk rot resistance and stalk breakage resistance made in maize hybrids devoted to both grain and silage use have likely lead to unfavorable effects on plant digestibility.

The physiological reasons leading to forage maize agronomic value improvements are not completely understood. However, just as future improvements in forage maize feeding value are related to a better understanding of cell wall biogenesis, future improvements in maize agronomic value are dependent upon a better knowledge of maize physiological processes related to yield and yield stability. Moreover, future improvements in forage maize agronomic values must be well balanced with more sustainable plant cropping managements, and with a simultaneous improvement of plant feeding values. Comparisons of old and modern hybrids contribute highlighted physiological traits modified during 50 years of breeding processes. Cold tolerance was improved with a better plant growth, including root growth, during spring (early vigor), and a better tolerance to chilling injury during grain filling and ripening. In parallel with stay-green improvement, leaf area duration is certainly significantly higher in modern hybrids compared to old ones, allowing a longer duration of photosynthesis. Leaves of modern hybrids are more erected with a higher interception of photoactive radiations. Modern hybrids are also later flowering, with a correlative higher leaf number and leaf area index, with a faster grain filling and ripening. Modern hybrids have a significantly higher stress tolerance (TOLLENAAR and WU, 1999), and do recover better from stress (TOLLENAAR *et al.*, 1994). Nutrient and water uptake is related to root mass and energy supply. TOLLENAAR and MIGUS (1984) showed that the root/shoot ratio was about 20% greater in a modern hybrid compared to an older one during the grain filling period. Higher source/sink ratio in more recent hybrids may imply a greater supply of assimi-

TABLE 3 - *Genetic improvement of maize whole plant yield in France. Estimates are based on official results for the best registered hybrid in each maturity group between 1986 and 2004. Year reassemblies correspond to each significant breaking steps in forage maize breeding.*

very early hybrids		early hybrids		medium early hybrids	
Registration Years	Yield % LG2080	Registration Years	Yield % Lixis	Registration Years	Yield % Dea
1986-1987	101.0	1986-1987	102.5	1986-1989	102.6
1988-1996	109.4	1988-1996	111.9	1990-1994	106.1
1997-2004	117.0	1997-2004	120.1	1995-2000	111.5
				2001-2004	119.9

lates to the roots (Rajcan and Tollenaar, 1999a). Correlatively, Rajcan and Tollenaar (1999b) observed that in a modern hybrid 60% of grain N derived from post-silking N uptake, whereas it was only 40% in the older hybrid.

Maize is sometimes considered as a non-sustainable crop, because of its summer needs of water during flowering and grain filling, therefore often requiring irrigation to prevent summer water stress. The water use efficiency in maize is yet the highest among plants, as in all species having C4 type photosynthesis (sorghum, sugarcane, …), and reaches 42 kg DM/ ha per mm of water used (Labarde, 2000). However, water resources are limited and a future continuous yield improvement has to be reconsidered. The water needs of hybrids such as Inra258 and LG11 were close to 300 mm, close to 400 mm for Dea, and between 450 and 500 mm for highly productive hybrids such as Anjou285 and later registered hybrids. The yield potential of maize under optimal conditions with respect to temperature and radiation in northern environments was estimated to be between 30 and 35 t/ha. The correlative water need of hybrids reaching the potential would thus range between 750 and 875 mm, which is much more than water availability in temperate environments. If water use efficiency was likely to not be improved by breeding in modern hybrids, or only very little, as it is the case for such biological constants, modern maize has an improved root system enabling a better use of water resources. Guingo *et al.* (1998) demonstrated genetic variation for root traits without colocalisation between QTL for DM yield and QTL for root traits. Landi *et al.* (2002) then established than several QTL for root pulling resistance, which is related to root development and architecture, overlapped with QTL for grain yield in water-stressed growing conditions, but not with QTL for grain yield in well-watered growing conditions. A more developed root system allows a better and deeper exploration of soil resources (Tuberosa *et al.*, 2002). However, the nitrogen content of water in deeper soil can be low, and nitrogen starvation can affect maize plants to a greater extent than water starvation. Whether roots of modern hybrids also have a higher intrinsic efficiency to take water is seemingly still unknown. Among physiological processes affected by water deficit, leaf growth is a sensitive one, with reductions in leaf expansion often occurring before any reduction in photosynthesis or in root growth (Westgate and Boyer, 1985). Substantial variation for leaf growth maintenance under water deficit has been observed in temperate maize germplasm. QTL of response of leaf growth to soil and air water deficits have been detected (Reymond *et al.*, 2003). Traits such as early vigor, deep rooting or preservation of leaf growth are obviously of interest in forage maize breeding. However, most of past or in progress investigations for evidencing physiological mechanisms or traits related to maize drought tolerance are related to grain filling and grain production, rather than to whole plant growth and biomass production. Tropical maize OP varieties or landraces often subjected to water stress should constitute the most evident genetic resources in breeding maize preserving yield under moderated water deficit, as occurring in Europe. However, because maize in these areas is mostly grain maize used for human feeding, natural and human selections could have mostly favored, in these origins, traits related to grain filling and grain production. Consequently, improvement of forage maize for drought tolerance needs investigations, in these resources, of traits related to capabilities of preserving a whole plant yield across dry periods.

CONCLUSION

Since hybrid introduction in Europe in the early 1950s, there have been three successive periods of breeding, with impressive improvements of agronomic traits, but also with a correlative decrease of forage maize feeding value in most of European countries. Major changes occurred in germplasm of elite early and medium early elite lines, with an increasing importance of elite US bred medium late lines and hybrids. Flint parental lines are now introgressed of dent germplasm. Dent parental lines often related in the past to Wisconsin, Minnesota or Canadian origins are now mostly related to Iodent, BSSS and Lancaster germplasm. A reduction of genetic diversity of maize elite resources in more recent hybrids did not probably occurred, including in European early hybrids. New resources were regularly introduced in early forage maize breeding from US or central America, Canada, and central Europe. However, further germplasm evolution, and correlative genetic resources, should preferably targeted more specifically agronomic traits such as water and nitrogen uptake, root growth, yield standability and stress tolerance. In the next future, a forage maize ideotype will also have to find a better balance between agronomic and feeding values.

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