Forage maize in mild-temperate zones: breeding strategies for the near future

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ABSTRACT
In this paper “mild-temperate zones” refers to the regions found outside the tropics with moderate temperatures over a long period of the year and enough water available for the development of maize with a maturity range greater than FAO 800. Forage maize adapted to these situations should: (i) maximize ear and stover yields, (ii) have a proportion of grain that ensures a percentage of dry matter of approximately 35% at silage, (iii) maximize the digestibility of the stover, and (iv) not be stay-green to favor early harvesting. With the final aim of obtaining hybrids, it is suggested either the achievement of forage inbreds only from adapted materials or the introduction of exotic material into the process, which would increase stover yield in particular. Improved yields, especially stover yields, seen a realistic objective, as much progress could be expected by taking advantage of the heritability and heterosis of the traits involved. Advances in stover digestibility seem more difficult to achieve, owing to the low heritability of its components. The lack of heterosis in these traits would require selection within populations. Intrapopulation selection for increased Digestibility of the cell wall content is probably the best way to improve the stover digestibility. In order to maximize the Total Digestible dry matter yield, the most important components to improve are stover and grain yield, both in early and late materials. However, as this maximization cannot be achieved at any cost (whole-plant digestibility cannot drop below a certain level to favor high yields), the limits of stover and whole-plant digestibility significantly affecting animal performance need to be clearly established. Only through these studies will it be possible to construct a useful ideotype beyond academic speculations.

INTRODUCTION
Importance of forage maize in mild-temperate regions. In the mid-nineteenth century the use of maize for forage was widespread both in the United States and Europe. However, this application was seasonal, as only fresh maize was given to animals for forage. Improvements in silage preservation led to an explosion in the culture of forage maize. Publications by Goffart [1] and Lecouteux [2] were very influential in Europe, but perhaps their impact was even greater in the United States, where silage maize quickly became the crop of choice, with 2500 silos in Wisconsin alone by 1890 [3]. Silage maize has since become the main staple food for ruminants. Comparative studies of different varieties of silage maize carried out in the 1890s pointed out that the weight of the green plant was often a poor guide to the actual yield of nutrients [3]. It was also soon discovered that the more mature the crops were at the time of silage, the less material and nutrients were lost during storage, provided that the material was not too dry to be compacted in the silo [3].

In Europe, the culture of forage maize has been traditionally confined to cold areas where dairy-livestock industry based on pasturing had given way to more intensive forms based on storable forage. The northern half of France, Germany, the Netherlands, England, northwestern Spain, northern Italy, etc. have
been using early maize adapted to the local climate for many years. The same is true for Canada and the northern part of the United States. However, early material adapted to extreme conditions is not the only maize cultivated for forage. Indeed, there are many mild-temperate regions in the world where the dairy industry has expanded, including the Mediterranean basin and areas in the southern United States, Brazil, Argentina, Chile, South Africa, India, etc. So, there is a need for specific materials adapted to these regions and their obtaining need not necessarily follow the patterns established in colder regions. In fact, the establishing of milk quotas in some industrialized countries and the rising influence of conservationist movements will probably favor: (i) the recycling of dairy by-products in situ and (ii) a change of livestock policy toward reducing the amount of concentrated feed given to animals while increasing the amount of forage. This brings about a need for large quantities of high quality feed that are difficult to achieve with pastures, making maize the material of choice.

**Differential characteristics of mild-temperate zones.**

In this review, mild-temperate zones refers to non-tropical areas with moderate temperatures over a long period of the year and sufficient water available for the development of the maize crop. Throughout the period favorable for plant growth, these regions have more daylight hours than tropical regions do. As forage maize is harvested before the grain has reached physiological maturity, late to very late germplasm (FAO 800 or greater) can be used in these areas.

**Ideal characteristics of forage maize for cultivation in mild-temperate zones.** Since it became clear that early forage maize needed to be different from grain maize, several approaches to breeding it have been explored and developed [4,5,6]. At present there seems to be a general consensus that the Total Digestible dry matter yield (TDm) per hectare should be maximized, but with the following restrictions: (i) the percentage of dry matter should be between 30 and 37% to ensure proper preservation and ingestion [7,8,9], and (ii) a certain percentage of grain must be reached to ensure acceptable levels of digestibility and transformation in the animal. On the other hand, no conclusive tests to determine the interval of digestibilities within which maize can be used as a staple for ruminants have been performed, although the importance of the proportion of grain has probably been overvalued. Furthermore, the predictions based on digestibility and ingestion often do not agree with the findings regarding transformation into milk [10,11,12,13]. The available data suggest that the minimum acceptable proportion of grain in forage maize is approximately 40% [7,9,11].

All of these properties would also be required for an ideal maize cultivated in mild-temperate zones. However, there are some important differences with respect to early germplasm. For instance, one of the greatest concerns in cold regions (with a short or very short frost-free period) is to achieve enough dry matter content to ensure adequate silage. For this reason, we propose the following characteristics as the most important for an ideal forage maize adapted to mild-temperate zones:

i) Maximized ear and stover yield. This can be partly achieved by adjusting plant earliness to the growing period as far as possible, because of the strong correlation between earliness and yield.

ii) A high enough proportion of grain to get a percentage of dry matter of about 35% at silage and to reach a high enough global digestibility to maintain animal production levels. As not all livestock obtains the same benefits from forage [13,14,15], it might be worthwhile to consider different ideotypes for cattle and sheep.

iii) Maximized digestibility of the stover to enhance the whole-plant digestibility.

iv) Non stay-green germplasm. Stay-green is considered a positive trait in early materials as it increases yield and makes harvesting easier. However, for late material it is a drawback as late hybrids have a lower harvest index than early ones, and with the very late hybrids considered here, this is even more true. The stay-green trait for very late materials would force a delay in harvest time to achieve the optimal percentage of dry matter for silage.

**The current situation.** At present, the forage maize used most in temperate zones is somewhat later (if later materials are commercially available) and sometimes sown at a slightly greater density, than that planted for
grain. Following the trend established with early materials, seed suppliers have recently begun to provide information regarding stover development and stay-green trait in their catalogues, although no information is yet provided about the chemical composition of the stover or about the harvest index.

In light of the above-proposed ideotype, the procedure used by farmers to maximize TDDmY seems very inefficient. So, there are still many fields of research open for late materials. In this context, the following suggestions are proposed to advance in the obtainment of new forage maize adapted to mild-temperate zones.

VARIABILITY, HERITABILITY AND HETEROISIS OF TRAITS RESPONSIBLE FOR TOTAL DIGESTIBLE DRY MATTER YIELD
As mentioned above, the idea that specific forage varieties should be obtained for early maize is generally accepted [8,9,16]. This has led to consider stover digestibility as a criterion for the inscription of forage hybrids in the official catalogs of several central European countries [17]. In areas with milder climates, the topic is still controversial [18] and much attention is still being paid to the proportion of grain in the silage - [19], although interest has slowly shifted toward stover production and digestibility [20,21].

Total Digestible dry matter yield is the result of the equation ear yield x ear digestibility + stover yield x stover digestibility. Given that ear digestibility shows very little variation [22] even over a wide range of dry matter content [23,24,25], there are three components left to improve, bearing in mind the above-mentioned restrictions regarding to whole-plant digestibility, dry matter content, and grain proportion.

It is evident that improvements in grain and stover yield must be based on exploiting heterosis by hybrids. On the other hand, traits influencing the nutritive quality of the stover show no heterosis [26,27] and their improvement can only be achieved through selection within populations.

Given the characteristics of mild-temperate zones, there is a remarkable variety of germplasm that can be used; in addition to the germplasm typically cultivated in these areas (adapted), tropical germplasm (exotic) can also be used. Exotic germplasm has great difficulties in adapting to colder areas, often failing to flower in response to the change in photoperiod [28]. Furthermore, no significant increases in grain yields have been achieved through its culture [29,30,31]. On the other hand, the increased maturity range (as a response to long photoperiods in mild-temperate zones) and the great vegetative development that it allows can be advantageous [21]. This is especially favorable when the exotic germplasm is combined with adapted materials [32]. A review of germplasm suitable for obtaining forage maize for cultivation in mild-temperate zones must therefore deal with late adapted, exotic, and semi-exotic (cross between adapted and exotic material) germplasm.

1.- Adapted germplasm.

The OP varieties that have been used in developing the elite adapted inbreds for grain production have received little attention from the forage point of view (stover yield and nutritional traits of the stover). Meanwhile, there is plenty of information available regarding grain yield, the other basic component affecting the TDDmY.

i) Stover yield and digestibility.

A comparative study of BS13(S2)C4 and Lancaster Surecrop [33] showed that Lancaster had a shorter maturity range than BS13(S2)C4, but Lancaster plants were larger and both stover and ear yields were greater (Table 1). The population BS13(S2)C4 had a more nutritive stover, less variability for all traits studied, and a lower stover Digestible dry matter yield (Table 1).

Information is also available about the genetic structure of quantitative traits involved in forage production for the Lancaster variety. The heritability of stover yield ranges between 0.14 [34] and 0.59 [33], that of stover digestibility between 0.21 and 0.23 [34], that of stover Neutral Detergent Fibre (NDF) between 0.32 [33,34] and 0.37 [34], that of the stover Digestibility of the cell wall content (DwCw) between 0.27 and 0.47 [34], and that of TDDmY between 0.22 and 0.26 [34]. Theoretically, all these traits should respond to selection as the population shows abundant phenotypic variance for them.

ii) Ear yield.

Ferret et al. [33] found an ear yield heritability of 0.30 for the Lancaster variety harvested at the optimal stage for silage, while Almirall et al. [34] found heritabilities of 0.21 and 0.29 for the same variety and harvesting
Table 1.-Comparison of mean phenotypic values between the populations Lancaster and BS13(S2)C4 [33]

<table>
<thead>
<tr>
<th></th>
<th>Lancaster</th>
<th>BS13(S2)C4</th>
<th>Student’s Test</th>
</tr>
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<tbody>
<tr>
<td>Days to pollen</td>
<td>62.92±0.37</td>
<td>67.93±0.30</td>
<td>0.01</td>
</tr>
<tr>
<td>shedding</td>
<td></td>
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<tr>
<td>Stover yield</td>
<td>158.46±5.81</td>
<td>127.85±4.31</td>
<td>0.01</td>
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<tr>
<td>(g/plant)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Stover dry matter</td>
<td>47.98±0.66</td>
<td>52.34±0.49</td>
<td>0.01</td>
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<tr>
<td>digestibility (%)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Stover Digestible dry</td>
<td>76.02±2.54</td>
<td>66.91±1.82</td>
<td>0.05</td>
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<tr>
<td>matter yield</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>(g/plant)</td>
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conditions. Many estimations of heritability have been calculated from material harvested for mature grain in medium-late varieties. Hallauer and Miranda [35], summarizing data from various authors, reported heritabilities ranging from 0.17 to 0.89 for ear yield, depending on estimation methods, for Iowa Stiff Stalk Synthetic. For Krug Yellow Dent and Hays Golden, Lindsey [36] found a predominance of additive genetic variance over dominant genetic variance; similar findings have been reported for the varieties Golden Republic and Barber Reid [37], Jarvis and Indian Chief [38], and Minnesota Synthetic 3 [39]. If the estimated heritability of grain yield were similar to the heritability of ear yield in silage maize, a generalized response to selection in all important late OP populations that would bring about an increase in the TDDmy should be expected.

2. Exotic and semi-exotic germplasm.

Interest in introducing exotic material in temperate zones to broaden the genetic base of materials currently used dates from the 1950s [40,41,42,43]. Nevertheless, the first studies to evaluate these materials for forage were not conducted until 1968 [44]. More recently, these materials have been proposed as candidates for cultivation along the Coastal Plain Region of the southeastern United States [21,45,46] and in mild Mediterranean climates [32].

i) Stover yield and digestibility.

There is very little information available about genetic variation for either stover yield or digestibility in exotic and semi-exotic populations. In fact, important differences have been found between semi-exotic populations with regards to the mean phenotypical value of both traits [32]. As for variation within populations, Mas et al. [47] studied the semi-exotic Mo17 x Across 8443 La Posta and estimated heritabilities of 0.44 for stover yield, 0.09 for stover NDF, 0.13 for stover digestibility, 0.15 for stover Dcw, and 0.21 for the TDDmy.

ii) Ear yield.

As in adapted populations, grain production is the aspect that has been most thoroughly investigated. Subandi and Compton [48] studied the variability of the population formed by the Canadian variety Gaspe crossed with three South American varieties (ETO, Narido 330, Peru 330). After a light selection process for adaptation to the environmental conditions of Nebraska, the estimation of the variances of the new population showed higher values of additive genetic variance than dominant genetic variance for grain yield. However, Mas et al. [47] in the population Mo17 x Across 8443 La Posta, harvested at the optimal stage for silage, found a heritability of 0.09 for ear yield with practically no additive variance. Albrecht and Dudley [49,50] found that the mixture of adapted and exotic materials increased genetic variability for production. Similarly, Iglesias and Hallauer [51] obtained a good response to selection for grain yield in the first selection cycles in a population formed by 50% exotic material and 50% adapted material.
BREEDING METHODS

1.-Breeding adapted populations.
The most logical starting point would be the varieties that have been used successfully to produce inbreds for grain production. As grain is an important component of forage maize, selection for forage traits in varieties such as Iowa Stiff Stalk Synthetic or Lancaster Surecrop would enable the attainment of superior inbreds very likely enriched with genes favoring grain yield. In the Lancaster variety, Ferret et al. [33] estimated the increase per cycle and unit of intensity of applied selection to be 15% for stover yield, 9% for ear yield, and 3% for stover NDF. In the same variety, Almirall et al. [34] estimated the increase per cycle and unit of intensity of applied selection to be 4-6% for stover yield, 7-9% for ear yield, 1.7-2.6% for stover digestibility, 2.4-2.6% for stover NDF, 3-6% for stover Dw, and 6-7% for TDDm. The traits involved in the nutritive quality of the stover had the lowest expected response to selection in both studies, and as mentioned before, showed no heterosis. These traits have the additional drawback of being difficult to measure, making it hard to work with a large number of plants. Moreover, as in selection for yield, these traits are recorded on harvested plants, making it impossible to cross the selected individuals. So, it is very important to find traits having good additive genetic correlations with TDDm (through one or more of its components) that can be easily measured before flowering. The additive genetic correlations between some morphological traits of the plant and TDDm make indirect selection through these traits advisable; the diameter of the base of the stalk and the plant height are especially noteworthy [34]. The efficacy of selection for greater diameter of the stalk as a means of increasing the TDDm was tested over successive selection cycles for the Lancaster variety, where an increase of 23.5% in the TDDm after five cycles of selection for stalk thickness was achieved [52]. No morphological traits genetically correlated with traits involved in the nutritive quality of the stover have been found [33,34,53]. Therefore, the increase in TDDm is achieved primarily through increased yields of both ear and stover. One consequence of selection for stalk thickness is a lengthening of the plant maturity range, as stalk diameter also has an additive genetic correlation with earliness. This correlation, however, is not as strong as that between plant height and earliness [34].

In late North American populations, selection for grain was successfully carried out by obtaining inbreds from base populations. Afterwards, recurrent selection by combining ability was performed to obtain superior inbreds. The most convincing evidence of this progress is that a large number of the elite inbreds involved in the best commercial hybrids have been obtained by selection within these populations. Furthermore, additional increases in yield achieved with new hybrids continue to be seen [54,55]. As ear yield is highly correlated with stover yield [33,34], selection for grain within a population should also drag along a favourable increase in stover yield.

Considering the slight influence of the nutritive traits of the stover in TDDm [33,34] and the difficulty of their measurement, it seems better to try to increase ear yield first, stover yield next, and finally, the nutritive quality of the stover. From a practical point of view, it seems advisable to use indirect selection to increase yields and to postpone the improvement of the stover nutritive quality. Recurrent selection by specific combining ability appears to be the most efficient method to progress in the attainment of forage lines using exclusively adapted materials. The use of only this germplasm avoids the adaptation process and ensures a beginning with populations already greatly improved for grain production. As seen before, this is not incompatible with stover production.

2.-Breeding exotic and semi-exotic populations. Several authors have recommended the use of exotic material to increase the variability of the germplasm currently used to improve maize (see previous section), and especially forage maize [56,57,58,59]. However, it is still uncertain what the most favorable proportion of exotic to adapted material would be [50,60,61,62]. On the other hand, information is starting to become available regarding the best heterotic patterns between exotic and adapted inbreds for grain production [63,64,65,66] and forage [20].

In the semi-exotic population Mo17 x Across 8443 La Posta, increases were expected on ear yield (3.7% per unit of intensity of selection applied per cycle), in stover yield (13%), in stover NDF (0.4%), in stover digestibility (1.4%), in stover Dw (1.8%) and in TDDm (6%) [47]. This population is a very promising exotic x adapted germplasm that responds especially
well to direct selection for stover yield, while the traits related to the nutritional value of the stover have a very weak response.

Indirect selection through highly correlated yield characters leads, as in the case of late adapted material, to traits such as stalk thickness or plant height [47]. In the case of indirect selection for increased diameter of the stalk, increases in the TDDmy of 4.18% per unit of intensity of applied selection and cycle can be expected, while the same selection pressure applied in plant height would be expected to give an advance of 4.62% [47]. As in the case of Lancaster mentioned above, selection for diameter only delays plant flowering by 1.39%, whereas selection for plant height delays flowering time by 2.35% per unit of applied intensity of selection and cycle.

Here again, improving the nutritional quality of the stover seems an inefficient approach to increase the TDDmy because these two traits, unlike TDDmy and yields, are not correlated. So, in the exotic and semi-exotic material, yields are also the best traits to improve TDDmy.

As far as breeding methods are concerned, the obtainment of inbreds to produce hybrids is still the best election, as car and stover yields are heterotic traits. It seems advisable to improve exotic or semi-exotic populations to derive exotic or semi-exotic inbreds and hybrids especially for forage use. Taking advantage of the good combining abilities of the exotic population Across 8443 La Posta, studies are underway to decide the best starting point for breeding. Either Across 8443 La Posta itself or a semi-exotic population obtained by crossing an adapted inbred with Across 8443 La Posta are good candidates [67,68]. The results up to now seem to favor semi-exotic populations as the starting point for selection in order to obtain a final hybrid of the type semi-exotic x adapted inbred [69,70].

As the objective is to develop late forage hybrids, a more complex programme would include the use of two adapted lines and two exotic populations (Figure 1a). These adapted lines and exotic populations should combine well for grain production. For example in Figure 1a, exotic A and Line 1 should combine well with both exotic B and Line 2. With this scheme fast advances in the recurrent reciprocal selection from two semi-exotic populations would be expected. The case described in Figure 1b guarantees a greater proportion of adapted germplasm in the final hybrid and a faster process. From the available information [32,67,68] it is reasonable to use for instance B73 and Mo17 as adapted inbreds, while Compuesto Centroamericano A, V464 and V465 (presumably Cateto), Across 8443 (Tuxpeño), and Brazil 1771 (Cateto) could be used as exotic material.

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Figure 1.-Two possible strategies for an improvement program, L1 and L2 being adapted complementary inbreds; exoticA and exoticB, complementary exotic populations; semiexA and semiexB, semi-exotic populations; sel1 and sel2, semi-exotic lines; and selHyb, semi-exotic hybrid.
SOME REFLECTIONS ABOUT THE NEAR FUTURE

The evidence shown so far suggests that the best way to achieve forage maize adapted to mild-temperate zones is a breeding strategy based on increasing ear production first, stover production next, and lastly the nutritional quality of the stover. Attempts at improving yields, which are very complex traits, will probably continue to use classical methods. Nevertheless, selection assisted by molecular markers has already been used, mainly for improving grain production [71,72,73,74,75,76,77,78,79,80] but also for improving forage maize [81]. Furthermore, there remains the possibility that molecular markers associated with morphological traits correlated to yield (such as plant height [82], number of leaves, or the diameter of the stalk), might also be useful for the indirect improvement of yields.

The available evidence suggests that the role of the nutritional quality of the stover in the TDD my is a minor one as the traits involved in the nutritional quality of the stover are not well correlated with TDD my (although they obviously play a role in the digestibility of the stover) [32,33,34,47]. Moreover, these are low heritability traits [32,33,34,47] and they are difficult to measure, even considering the generalization of NIR methods in their estimation [83,84,85]. Although these traits are not easy to improve, they cannot be ignored as stover quality is essential to maintain an acceptable level of whole-plant digestibility if the harvest index is reduced. This reduction will happen as advances in stover production are more likely than advances in grain production. Furthermore, stover from late materials has been reported to be less digestible than from early materials. Thus, while Ferret et al. [33], Bosch et al. [20], Bosch et al. [32], and Almirall et al. [34], found that stover digestibility ranges between 46 and 53% in materials later than FAO 700, Deinum [86] found values of between 62 and 64% in FAO 200-300 hybrids.

Considering all this, stover Dcwc seems to be the best choice to improve stover quality. This trait has proven to be more heritable than stover digestibility or the proportion of cell wall (NDF), probably because it is the trait that is least affected by the environment and grain production [16,22,34,57].

Apparently, stover Dcwc is an easier trait to deal with than stover digestibility. This has led to several analytic attempts to identify the chemical components responsible for stover digestibility. So far the results are inconclusive, but it seems that lignin content and etherified ferulic acid content, which probably acts as a bridge between lignin and hemicellulose, are what bring about the greatest decrease of the Dcwc [88,89,90,91,92,93]. The kinetics of Dcwc degradation and the breakdown of its molecules in ruminal liquid are also being studied. Preliminary findings suggest that there is considerable variation for this trait [94,95,96,97]. At the same time, genes responsible for lignin synthesis are starting to be identified [98], which allows a new approach for improving digestibility.

To sum up these reflections, it is convenient to go back to one of the gray areas in the improvement of forage maize. It has been assumed in this exposition that within certain limits of whole-plant digestibility and dry matter content (both strongly related with the harvest index), the most important objective was to increase total yield. The remaining problem is to determine the optimal ranges of stover and whole-plant digestibility for transformation into milk or meat. On the other hand, it is true that there are many analytic values, even in vitro, that demonstrate the existence of variability in digestibility among materials. This can be measured with relative ease by evaluating the nutritional traits of the stover in the laboratory. The question is, however, to what extent these differences are important in transformation within animals. Very little information is available about this topic, and experiments on animals are difficult and expensive. So far, it has been shown that there is no difference in milk production in cows fed forage with a proportion of grain of 41 and 50% [11,12]. These findings contrast with results obtained for sheep, which seem to be more sensitive to grain content. So, the only useful application of findings in sheep for milk production in cows is to separate materials with extreme differences in digestibility [13]. Cows apparently take more nutritional benefits from the stover when the proportion of grain is reduced [11]. In spite of these data, it seems clear that further studies are necessary to establish these limits, which will determine the definitive strategies for the improvement of forage maize in the immediate future.

Finally, digestibility is another aspect that needs to be studied in greater depth. Due to its complexity,
ingestibility has been left out of the main experimental programmes and should be one of the primary objectives of research in the near future.

EARLY AND LATE FORAGE MATERIALS

Studies of the relative importance of the different components of whole-plant digestibility in forage maize seem to give contradictory results depending on the earliness of the materials studied. Indeed, the prevalent idea among authors working with early material was, until recently, that efforts should be devoted primarily to improving the digestibility of the stover [86,99,100,101], whereas breeders working with late materials continue to place the greatest emphasis on the importance of the proportion of grain [18,19,102,103].

This apparent paradox seems to have a simple explanation. In fact differences are also found among studies performed in early materials. Deinum and Struik [104] point to the digestibility of the stover as the key element in whole-plant digestibility (=0.66 between these two traits), while the correlation between proportion of ear and whole-plant digestibility is only 0.47. In another study, Deinum [86] found a correlation of 0.57 between stover Dcw (highly correlated with stover digestibility) and whole-plant digestibility, while the correlation between ear proportion and whole-plant digestibility was only 0.38. Similar data have been reported by Deinum and Bakker [22] and by Vattikonda and Hunter [105].

In contrast, Beerepoot [106] found a correlation of 0.56 between stover digestibility and whole-plant digestibility in early materials and a correlation of 0.69 between whole-plant digestibility and ear proportion. These results are in agreement with those by Geiger and Seitz [107].

The results found in late materials are even more striking with respect to the generally held belief. In a study of 21 commercial hybrids, Bosch et al. [20] found a correlation of 0.94 between stover digestibility and whole-plant digestibility, while the correlation between whole plant digestibility and ear proportion was only 0.16. On the other hand, Bosch et al. [32], in semi-exotics materials found a correlation between whole-plant digestibility and stover digestibility of only 0.12, while the correlation between whole-plant digestibility and ear proportion was 0.73. These results are in agreement with the findings of Almirall et al. [34] in the Lancaster variety, with correlations between whole-plant digestibility and stover digestibility of 0.43 and between ear proportion and whole-plant digestibility of 0.53.

The key to understanding these paradoxical results found in both early and late materials lies in the varieties studied. When dealing with highly improved materials like commercial hybrids [20,86,99,101] the importance of stover digestibility is predominant, probably because ear production has already been maximized, its proportion is already high, and it is a trait that shows little variability. On the other hand, when dealing with experimental materials [32,34,106,107] there is great variability in ear proportion. As the ear is highly digestible, ear proportion becomes the predominant element in whole-plant digestibility.

In most materials, TDDmY correlates best with stover and ear yields, regardless whether the materials are early or late, or whether they are highly improved or experimental. Working with early materials, Kappel et al. [108] found that TDDmY had correlations of 0.81 with ear yield, 0.73 with grain proportion, and 0.47 with stover yield. In late commercial hybrids, Bosch et al. [20] estimated correlations of 0.77 between TDDmY and ear yield, 0.44 between TDDmY and stover yield, 0.34 between TDDmY and ear proportion, and 0.34 between TDDmY and stover Dcw. In semi-exotics Bosch et al. [20], found a correlation of 0.82 between TDDmY and ear yield, 0.68 between TDDmY and stover yield, and 0.32 between TDDmY and ear proportion, whereas the correlation between TDDmY and Dcwce was -0.28. Finally, in the Lancaster variety, Almirall et al. [34] found a correlation of 0.95 between TDDmY and ear yield, 0.77 between TDDmY and stover yield, and 0.60 between TDDmY and ear proportion. The estimated correlation between TDDmY and Dcwce was 0.

We could conclude that: (i) There is no paradox between early and late materials. (ii) The factors that have the greatest weight in whole-plant digestibility are the digestibility of the stover (fundamentally the Dcwce) and ear proportion. The predominance of one or the other depends on the respective variability in the material studied independently of plant earliness. (iii)
Total Digestible dry matter yield depends on ear and stover yields in most cases, and the digestibility of the stover normally has much less impact on this trait, so it seems clear that the best way to maximize TDDmy is to increase yields. Nevertheless experiments with animals need to establish the limits of whole-plant digestibility affecting transformation, the intervals of difference in digestibility perceived by ruminants, and also, the effects of whole-plant digestibility and ear proportion on digestibility. Apparently, things are much clearer from the breeder’s point of view than from the point of view of ruminant physiology. In other words, specialists in animal nutrition need to contribute to the description of the ideotype for forage maize, as the transformation of vegetable matter into milk or meat is not simple. As was previously pointed out, this is where studies are most urgently needed to enable breeders to know exactly what to strive for.

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