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BREEDING AS A LEVER TO IMPROVE SEED YIELD OF FORAGE SPECIES

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Abstract

Breeding for seed yield is a lever that is not widely used. Indeed, the evaluation of seed yield components requires specific experimental conditions that come in addition to the ones used for the evaluation of forage-related traits. In addition, the genetic resistance to pests that are particularly damaging the plants at reproductive stages has not been much studied. Current knowledge is quickly reviewed and suggestions to implement molecular breeding are proposed. Selection for both forage and seed traits could be managed in cost-effective breeding schemes.

Introduction

Genetic improvement of forage species mainly targets forage yield, quality and stress resistances. Seed yield is a key trait for a variety to access the market (Boelt *et al.* 2015). As any other trait, seed yield can be selected to create new varieties (Wilkins and Humphreys 2003; Boelt *et al.* 2015). Seed yield results from components that start from flowering date and pollination to seed harvest. In addition to seed yield components, pests and diseases that are specific to reproductive stages, may alter seed yield potential. Knowledge of the genetic determinants of seed yield components is useful to create improved varieties. However, the selection for seed yield requires additional designs to those devoted to forage yield. Molecular markers could also help to introduce the selection of seed yield components in breeding schemes. The paper reviews current knowledge on seed yield of herbage species and possible changes in breeding schemes to improve genetic gain for seed production.

Why is it difficult to select for both forage and seed yield components?

For forage species, breeding for the traits that compose forage production such as forage yield and quality, are the main objectives. Recurrent breeding schemes are based on a breeding pool that is enriched with new introductions and produce candidate varieties and improved families that form the breeding pool for the next cycle of selection. The breeding traits are also evaluated during the Value for Cultivation and Use (VCU) tests that compose the process of variety registration on Official catalogues of varieties. The evaluation of forage related traits requires management practices and cutting schemes that are not those of seed production. Basically, plants are cut before or at the beginning of flowering. Consequently, seed yield potential is not fully targeted in the breeding schemes, and conversely, breeding for seed yield components requires specific managements within the breeding schemes.

Forage as well as seed productions are also submitted to pests and diseases. Some of them are common to both types of production while additional pests and diseases are specific to reproductive stages. Pesticides have been selected to fight against several pests that are

detrimental to seed production (Bouet *et al.* 2021; Gaier *et al.* 2022) but active substances are now banned one after the other because of their negative effects on human and environmental health. While management options may be available to limit pest damages (as an example, for *Hypera* on lucerne (Pellissier *et al.* 2017)), the genetic option is also an important lever to activate but this breeding objective is very recent.

Because of these constraints, breeding for seed production has not been invested much, as requesting dedicated efforts that come in addition to those devoted to forage traits improvement.

Seed yield components

Seed yield, as the seed weight per m² in dense canopy, is measured in small plot trials that mimics seed production fields; in a breeding scheme, it can be evaluated when enough seeds are produced, in the latest stages only. Breeding is the most efficient when the selection is applied in the earliest stages of a breeding scheme. The decomposition of seed yield into components is useful to identify traits that are easy to measure in a cost-effective way. Such traits must be correlated to seed yield. Seed yield components are defined at a biological scale, plants, stems, inflorescences, pods and seeds in legume species (Boelt *et al.* 2015), and plants, stems, inflorescences, spikelets, florets, seed set and seeds in grass species (Abel *et al.* 2017). Seed retention (grasses) and pod indehiscence (legumes) have been selected in modern germplasm. An efficient breeding criterion is a trait that shows a high genetic variation, a high genetic correlation with seed yield measured in plots and that is easy to measure, preferably in individual plants. The correlation between traits measured on spaced plants designs (the nursery in the early stage of a breeding scheme) and seed yield measured in dense canopy must also be high (Wilkins and Humphreys 2003). In several forage legume (Bolaños-Aguilar *et al.* 2000; Vleugels *et al.* 2016) and grass (Robins *et al.* 2015) species, seed traits measured at the inflorescence level have been shown to be an accurate breeding criteria. Comparison of varieties for seed yield to assess a genetic progress is not frequent. However, on perennial ryegrass, no genetic progress for seed yield has been reported among varieties bred for turf (Sampoux *et al.* 2013) or forage (Sampoux *et al.* 2011).

Pest and disease resistance

During legume seed production, several insects attack vegetative (*Agriotes* sp., *Apion* sp., *Colaspidema* sp., *Hypera* sp., *Sitona* sp., *Bemisia tabaci*) or reproductive (*Tychius* sp., *Contarinia medicaginis*, *Dasineura ignorata*, *Lygus* sp., *Adelphocoris* sp., *Bruchophagus* sp., *Cydia medicaginis*) parts of the plants while aphids (*Acyrtosiphon* sp.) suck sap of all green organs. Their occurrence varies depending on the environment, their impact on forage production is usually low or neglected and their negative impacts on seed production may be major. For some insects such as aphids and *Hypera*, protocols for variety testing are available (Girousse and Bournoville 1994; Ratcliffe 2022), by using insects raised in controlled conditions (aphids) or insects collected in fields (*Hypera*). In the USA, lucerne varieties are described for resistance to three aphid species and potato leafhopper (NAFA 2023). Insect damages on grasses are not frequent in Europe but well described in other regions of the world (Wilkins and Humphreys 2003). Generally speaking, more knowledge is needed on the biology

of pests to rise insects, develop protocols for variety testing and identify genetic diversity for insect resistance. Then, mechanisms of genetic control of resistance can be studied, possibly involving physical barriers such as trichomes (Gonzalez-Garcia *et al.* 2000) or biochemical compounds (Yan *et al.* 2023).

Disease occurrence is generally not specific to seed production but, as the growing period is longer than for forage production, their impact may be more important. For the main diseases in each species such as *Sclerotinia trifoliorum* on red clover, *Verticillium albo-atrum* on lucerne, anthracnose (*Colletotrichum trifolii*) on both red clover and lucerne, rusts on grasses, efficient selections are already conducted, aiming at a genetic progress. Disease tests are carried out under controlled conditions and resistant plants or progeny are introduced in the breeding scheme. In addition, candidate varieties that have been improved for forage yield components may be further improved for resistance to specific diseases before they are deposited for registration.

Implementation of molecular breeding

Molecular breeding has shown its efficiency to improve genetic gains in major crops. Recently, with genome-wide association studies (GWAS), loci (QTL) that explain more than 10% of the variation have been identified in forage crops too, mostly for forage-related traits (Keep *et al.* 2020; Pégard *et al.* 2021). Genomic selection seems promising, with predictive ability ranging from 20 to 70% depending on the studies and the traits (Annicchiarico *et al.* 2015; Keep *et al.* 2020; Pégard *et al.* 2021). Again, seed yield traits have been less studied than forage related traits or disease resistances. However, QTL have been detected in a bi-parental population of red clover for seed yield components (Herrmann *et al.* 2006). In a collection of perennial ryegrass, the QTL detected for spike density were explained by difference in earliness only and no QTL was detected for the other seed yield components (Keep *et al.* 2020). However, predictive ability for seed yield components was moderate to high (39% to 86%) (Keep *et al.* 2020).

Quantitative genetics, including GWAS and genomic selection, may also be efficient for resistance to diseases, as shown on red clover for anthracnose resistance (Frey *et al.* 2022). Resistance genes have been identified (Yang *et al.* 2022), they could be introduced through crossings but also by transgenesis (Tohidfar *et al.* 2013). No report for GWAS nor genomic prediction for resistance to pests on herbage crops has been identified so far in the literature.

Conclusion

Seed yield of herbage species results from seed yield potential and, especially for legume species, pest resistances. Both types of traits are complex to study and select for, and knowledge is lagging behind. Combination of selection for forage traits and seed traits in breeding programmes is costly while the seed market of forage species has a relatively low profitability. In these conditions, the development of tools for molecular assisted selection could help to improve seed yield. Such genetic progress could be acknowledged by the inclusion of seed yield in the evaluation of varieties for registration.

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