

Forecasting the impact of genomic selection on genetic gain in perennial ryegrass breeding

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Abstract

Simulation offers a way to explore questions about implementation, value and impacts of breeding methods for pasture species in New Zealand. The following genetic modelling summarised the potential of a small-scale application of genomic selection (GS) to improve breeding outcomes in perennial ryegrass (*Lolium perenne* L.), relative to conventional half-sib family genotypic selection, for dry matter yield (DMY). Predicted genetic gain (ΔG) for DMY in half-sib family genotypic selection without GS ranged up to 4.9% per cycle, depending on selection intensity. Coupling that with GS for within-family selection saw ΔG for DMY range up to 7.6% per cycle. Across nine scenarios tested for a single cycle with and without GS, increasing ΔG doubled the cost-efficiency per unit gain, even though cost increased. Simulation of 10 cycles of selection within the population at three selection intensities with and without GS showed higher ΔG were maintained over multiple cycles for GS. This highlighted the value of accuracy, selection intensity, speed of breeding cycles, and frequent refreshment of the GS model. Although gains were modest at this scale, this complemented empirical evaluations, indicating that incorporating GS in pasture breeding can increase rate and cost-efficiency of improvements, particularly when applied at scale.

Keywords: *Lolium perenne*, breeding, simulation, modelling

Introduction

Perennial ryegrass (*Lolium perenne* L., PRG) herbage is the main source of nutrition supporting production in New Zealand's animal-based dairy, meat and fibre industries. One aim of plant breeding, integrated with farm management, is to increase herbage production with similar or lower input levels per unit land area. Breeding progress over time is measured by rate of genetic gain (ΔG). For PRG, dry matter yield (DMY) ΔG has been estimated to be up to 0.7% per annum in New Zealand and overseas (McDonagh *et al.*, 2016). While this lags behind the rate of gain in species such as maize (Smith *et al.*, 2015), it has contributed substantially to improved economic returns from pasture-based primary production, already valued at

over NZ\$16 billion per annum (NZIER 2016).

Genetic improvement for other economic traits, such as nutritive value and vegetative persistence, have not been evaluated for historic rate of ΔG in Australasian PRG cultivars, but are a high priority for plant breeders and farmers alike. Alongside DMY, performance for these traits is being benchmarked in current PRG cultivars via the DairyNZ Forage Value Index (FVI), with these values based on an economic and cultivar performance model being developed to inform farmer and breeder decision making (Chapman *et al.*, 2017). In addition to continued improvement of ΔG for traits in the FVI, pasture plant breeding needs to rapidly respond to support farmers operating within environmental limits, and to improve pasture resilience in the face of climate change impacts.

Emerging technologies, including genomic selection (GS) as supported by high-throughput phenotyping (HTP), can markedly improve plant breeding efficiency (Crossa *et al.*, 2017). Genomic selection uses a mathematical model derived from DNA fingerprint and trait performance data for a reference set of individuals or families that is representative of a breeding programme. This model allows breeders to predict relative performance among large numbers of selection candidates from within the breeding programme based on DNA fingerprints alone, using Genomic Estimated Breeding Values (GEBVs) to inform selection decisions ahead of field evaluation. This approach has been developed and demonstrated empirically with a small reference population to increase response per selection cycle, compared to conventional family-based genotypic selection in PRG in New Zealand (Faville *et al.*, 2020; Faville *et al.*, 2021), and can increase ΔG by reducing generation interval and/or improving selection accuracy (Esfandyari *et al.*, 2020).

Concurrently, HTP has enabled breeders to improve the precision and cost-efficiency in field evaluation of DMY in PRG breeding trials, addressing a major bottleneck in pasture breeding systems (George *et al.*, 2019; Ghamkhar *et al.*, 2019). Creating a more precise, accurate, lower-cost and non-invasive basis for trait measurement makes HTP an essential enabler of GS, due to considerably larger multi-site phenotyping trials of reference sets being required to improve GS prediction models.

Convergence of the need to improve breeding outcomes across a range of PRG traits and the emergence of new breeding technologies raises questions around prioritisation and optimisation of technology implementation, and their expected impacts over time. Computer simulation has enabled exploration of the potential impacts from adopting new breeding technologies, with regards to the rate of ΔG in PRG, other genetic outcomes, and cost-efficiency. Such insight is useful when integrating new technology into breeding systems, helping forecast and prioritise outcomes. Simulation has already played a role in PRG research, indicating that GS can increase ΔG over time when compared to historic rates of gain, and that inbreeding effects associated with recurrent selection can be ameliorated (Lin *et al.*, 2016; Lin *et al.*, 2017a). Simulations have been used to estimate the point at which returns on investment to the breeder are optimised, showing that moderate sized programmes can improve outcomes (Lin *et al.*, 2017b).

Recently QuLinePlus, a new ΔG simulation module, has been developed for use in outcrossing species (Hoyos-Villegas *et al.*, 2019) such as PRG. This module enables analysis of genotype \times environment interaction effects in forecasting genetic response across multiple environments over multiple cycles of selection. Additionally, DeltaGen (Jahufer & Luo 2018) has been developed as a tactical decision-support freeware available to plant breeders and geneticists. DeltaGen enables deterministic simulation of genetic gain using real or experimental datasets to predict responses to selection and associated costs within a breeding cycle. The software deploys a range of breeding method algorithms which enable assessment of the relative efficiency of a wide range of selection strategies as measured by ΔG and cost per cycle. These tools have recently been used to explore impact of breeding method, accuracy and population size on rate of genetic gain and related outcomes in perennial ryegrass breeding (Jahufer *et al.*, 2021).

The objective of this paper was to investigate the projected impact over time of a specific small-scale application of genomic selection in a perennial ryegrass breeding population, as measured by the rate and cost-efficiency of gain, cumulative genetic gain and inbreeding effects, using two complementary simulation approaches.

Materials and Methods

Breeding simulations were conducted using a deterministic and a stochastic modelling approach, the latter enabling analysis of trends in genetic outcomes over multiple selection cycles. Results from deterministic modelling were based on field trial seasonal growth data, enabling empirical estimates of heritability, which

were used in generating an *in-silico* breeding population to conduct the stochastic modelling across multiple breeding cycles. This enabled stochastic modelling to be carried out on a population with similar genetic parameters to that used in the deterministic method.

The objective of the simulation was to assess relative predicted ΔG and cost per cycle of selection for two breeding methods, either conventional genotypic among half sib (HS) family selection using phenotypic information (HS_p), or the combination of among HS family selection using phenotypic information and within HS family selection using GS ($A_p WF_{gs}$). Standard definitions were used for these methods (Casler & Brummer 2008), noting that GS enabled selection for sward traits among individuals without the need for progeny testing. The number of years per cycle was assumed to be the same for both methods.

Deterministic simulation of genetic gain.

All deterministic simulation was conducted using DeltaGen software (Jahufer and Luo 2018), and simulated gain in progeny of the same base population that was used to derive the GS model. Simulations were based on two years of PRG calibrated seasonal growth score (1, low to high, 9) data, collected from a multi-year HS family evaluation at Ruakura (Waikato region, New Zealand, 37.78°S, 175.32°E; Te Rapa peaty silt loam). Calibrated growth score is an indirect measure of DMY, often used in PRG breeding systems to estimate relative differences among families or populations (Smith *et al.*, 2001). The data were collected from 98 HS families sampled from a commercial breeding population named 'Pop III'. Full information on Pop III data, including trial site and experimental protocols, has previously been presented in Faville *et al.*, (2018).

A linear mixed model analysis using the Residual Maximum Likelihood (REML) procedure in DeltaGen was used to analyse the HS family growth score data. The estimated genetic parameters for growth score and interaction effects were then used in deterministic modelling equations for HS_p and $A_p WF_{gs}$ breeding strategies, as described by Jahufer and Luo (2018).

For modelling within HS family genomic selection, prediction accuracy was set at $r = 0.26$, a level in the mid-range of values reported in empirical studies (Faville *et al.*, 2018). The cost of generating a GEBV was set at \$41 which was inclusive of growing the plant material, extracting DNA, making and sequencing genotyping by sequencing libraries. This was followed by bioinformatic analysis to identify the DNA fingerprint, which was used in prediction modelling to derive and estimate phenotype. Other costs for breeding data were per sample score per season, per replicate per year, per location per year and general costs across both years, which were estimated at \$0.50, \$500, \$25,000

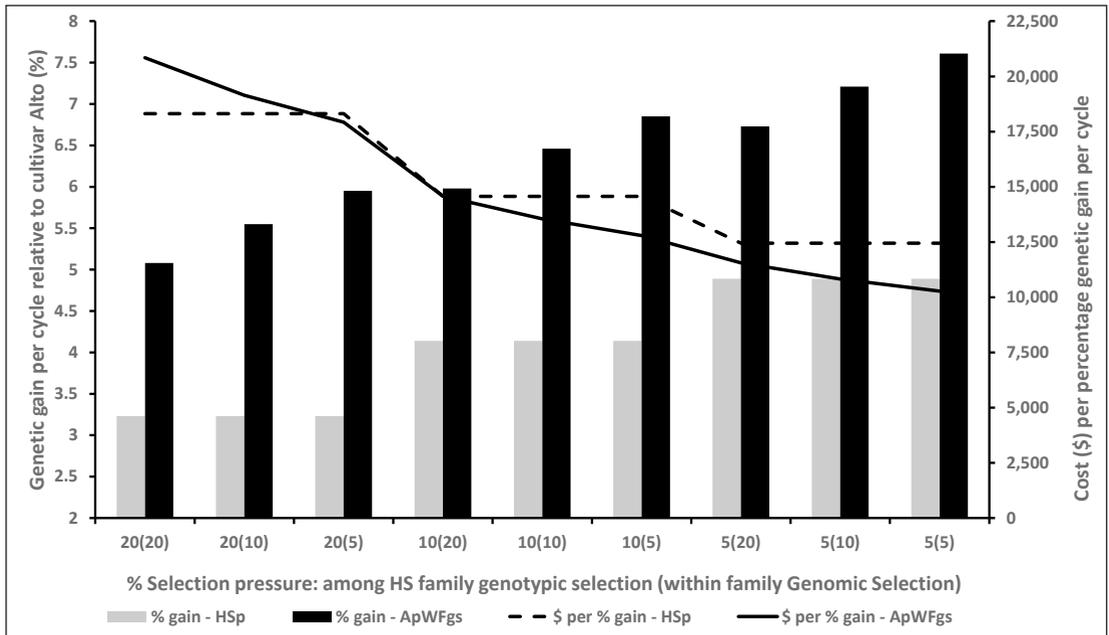


Figure 1 Percent genetic gain (left axis) and breeding cycle costs (right axis) in a commercial population under nine different selection methods, expressed relative to cultivar Alto AR37, using simulation of a single cycle of selection with and without genomic selection. The source data are seasonal growth score data from 98 HS families evaluated in field trials for two years at Ruakura. Breeding methods simulated were among HS family genotypic selection (HS_p); and a combination of among HS family genotypic selection and within HS family genomic selection (A_pWF_{gs}).

and \$10,000, respectively. Perennial ryegrass cultivar Alto infected with the AR37 strain of fungal endophyte (*Epichloë festucae* var. *lolii*) was used as a benchmark to express predicted percentage ΔG per cycle of selection, as it was included in the original field trials. In this experiment the seasonal growth score average for Alto AR37 was 6.3. The selection intensities modelled included all nine pairwise combinations of 20%, 10% and 5% among-family, with 20%, 10% and 5% within-family.

Stochastic simulation of genetic gain

Stochastic simulations were used to evaluate longer-term genetic outcomes for HS_p and A_pWF_{gs} applied within a breeding population, assuming both breeding methods required three years per cycle. Three levels of increasing selection pressure were tested; lowest pressure of 20% among and 3.33% within, 10% among and 6.66% within, and highest pressure of 5% among and 13.33% within, in all cases using 150 selection candidates within family. The within-family selection pressure was set in relation to the among family pressure at a level that provided for a constant number of parents to be selected in each cycle. Genetic response trends to selection including $\% \Delta G$, allelic fixation rate, genetic variance and prediction accuracy were each estimated across 10 selection cycles using QuLinePlus software

(Hoyos-Villegas *et al.*, 2019) with modifications to implement a simulation of GS.

Simulations used a new initial breeding population derived using the genetic parameters of the PopIII empirical dataset described above. QuLinePlus was used to generate 98 HS families based on the genomic and trait data from the initial population. These HS families were simulated for their performance and growth scores across three years. From each of the evaluated families, a random individual was drawn to form a training population of 98 plants, consistent with the population size used in deterministic modelling above.

For simulating trait response to selection, QuLinePlus required a genome map that included the location and effect of genetic loci influencing growth score. The genome map and genetic loci information were obtained from a genome-wide association analysis of the initial population, using previously recorded growth scores and genotype DNA marker information, as described in Faville *et al.*, (2018). Growth score heritability was set at the same level used in the deterministic modelling.

Results

For the deterministic simulation of genetic gain, variance component analysis of the multi-year and season growth score data indicated significant ($P < 0.05$)

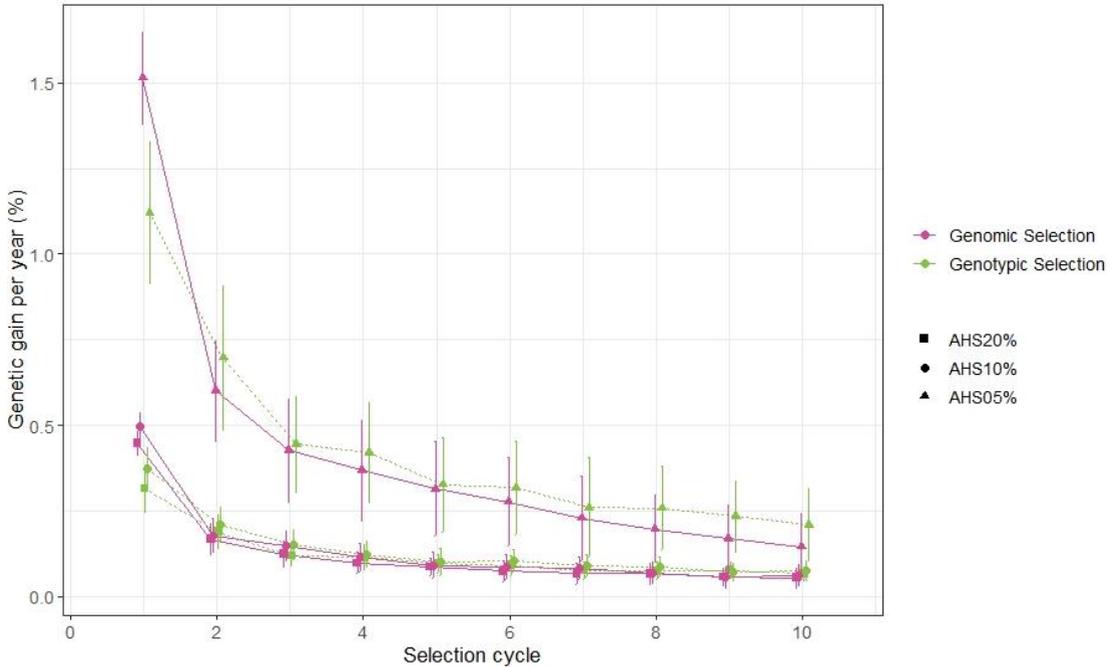


Figure 2 Genetic gain per year (% +/- Standard Error of the Mean) across 10 selection cycles using among-family genotypic selection and within-family genomic selection, A_pWF_{gs} (Genomic Selection); and conventional half-sib family selection, HS_p (Genotypic selection) at three selection pressure combinations: ■ 20% among and 3.33% within, ● 10% among and 6.66% within, and ▲ 5% among and 13.33% within.

additive genetic variation ($\sigma^2_A=0.136\pm 0.026$) among the 98 HS families. The estimated narrow-sense heritability on a HS family mean basis was 0.734 ± 0.051 .

Predicted % ΔG for nine different combinations of selection pressure and associated cost per percentage genetic gain are shown in Figure 1. Applying the HS_p breeding method at increasing selection pressures of 20%, 10% and 5% increased ΔG by 3.2%, 4.1% and 4.9%, respectively, compared to the benchmark cultivar Alto AR37. When GS within the selected elite HS families was included, predicted ΔG increased. This ranged from 5.1% for the combination of 20% among and within family selection pressure combination, up to 7.6% for the 5% among and within combination. Increasing selection intensity increased ΔG and halved the estimated cost per unit genetic gain from over \$20,000 to less than \$10,000 (Figure 1).

Genetic responses to multiple cycles of selection under HS_p and A_pWF_{gs} at three different selection pressures was explored using a stochastic model with data derived from Pop III, a commercial breeding population. The simulation ran for ten selection cycles within the population, maintaining a constant number of parents per cycle. The application of this approach resulted in selection pressure combinations of 20% among family and 3.33% within, 10% among and 6.66% within, and 5% among and 13.33% within. Output data

included ΔG per cycle (Figure 2), accumulation of ΔG (Figure 3), and proportion of fixed favourable alleles (Figure 4). Genetic gain per cycle was higher for GS in the first cycle, and, while it decreased over the cycles of selection, positive response to selection was observed in each cycle.

The model indicated a similar ΔG response for the 20% and 10% among-family selection pressures, whereas the 5% selection pressure markedly lifted the response to selection (Figure 2). When assessing cumulative ΔG , the model indicated GS was highest at selection cycle 1 for all three selection pressures (Figure 3). From cycle 2, although GS contributed to ΔG , the difference in gain per cycle was larger for genotypic selection and matched the GS approach at selection cycle 10 (Figure 3). In contrast, the rate of favourable allele fixation (%) varied among the three among-family selection pressures, 20%, 10% and 5% (Figure 4), with 5% achieving the highest fixation rate at all selection cycles.

Discussion

Simulation offers ways to gain insight into genetic outcomes enabled by changes in pasture plant breeding systems. The genetic simulations reported here indicated that, in cases where there was a high degree of relatedness between the selection candidates and the

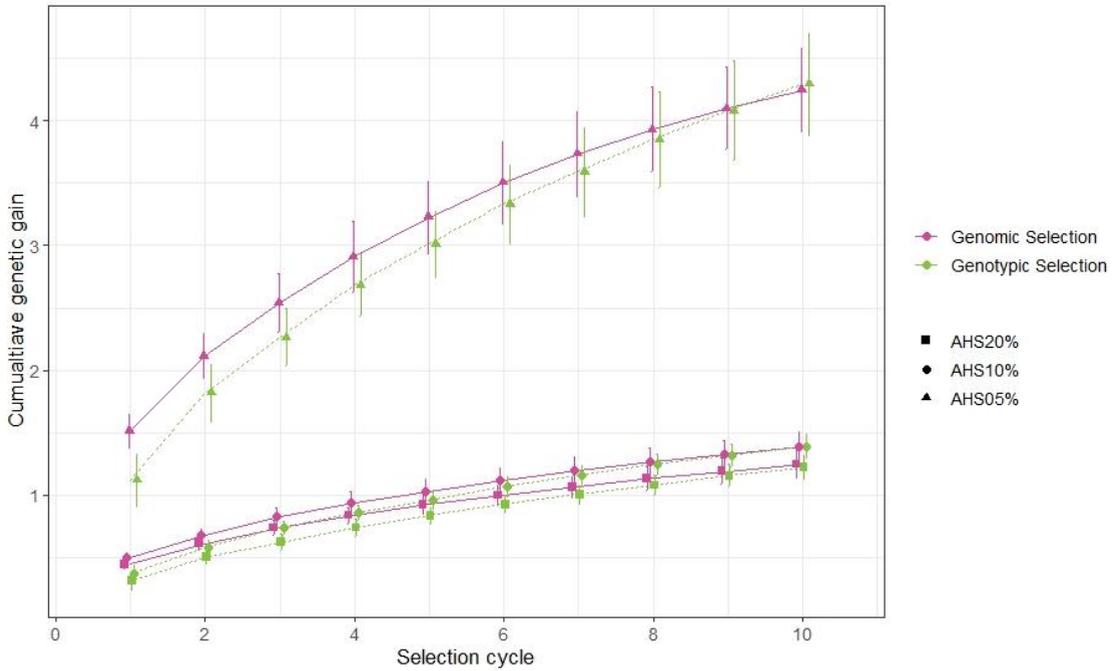


Figure 3 Cumulative genetic gain (% +/- Standard Error of the Mean) across 10 selection cycles using among-family genotypic selection and within-family genomic selection, $A_p WF_{gs}$ (Genomic Selection); and conventional half-sib family selection, HS_p (Genotypic selection) at three selection pressure combinations: ■ 20% among and 3.33% within, ● 10% among and 6.66% within, and ▲ 5% among and 13.33% within.

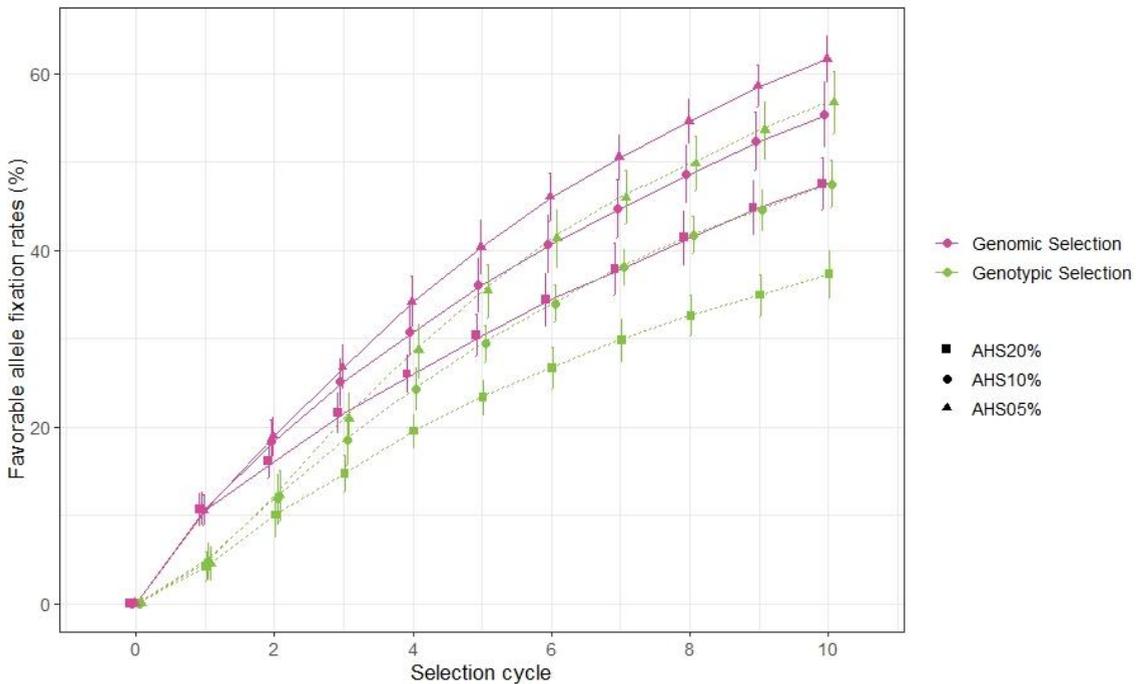


Figure 4 Allelic fixation rate of favourable alleles across 10 selection cycles using among-family genotypic selection and within-family genomic selection, $A_p WF_{gs}$ (Genomic selection), and conventional half-sib family based genotypic selection, HS_p (Genotypic selection), at three selection pressure combinations: ■ 20% among and 3.33% within, ● 10% among and 6.66% within, and ▲ 5% among and 13.33% within. Error bars are standard error of the mean.

reference population used to train the model, GS can double ΔG in the first cycle when compared to *HSp* (Figure 1). This continued to deliver gains over multiple selection cycles, albeit with diminishing returns per cycle (Figures 2 and 3).

The determined improved cost efficiencies at higher rates of ΔG was broadly in line with other simulations (Lin *et al.*, 2017b) using independent computational tools and assumptions. This supported the conclusion that, to achieve optimal return on investment, it was necessary to pursue a GS strategy at or above a minimum threshold scale.

The findings of this study, using data from existing commercial breeding populations, were broadly in line with other simulation examples in pasture plant breeding (Lin *et al.*, 2016; Esfandyari *et al.*, 2020) that relied on theoretically-derived artificial base populations. The populations used in the simulation were derived from empirical data from field trials and used relatively few selection candidates, in line with research scale implementation of GS.

This limited scale of application gave rise to a number of constraints on the potential impact of GS on genetic gain. The decline in increment of genetic gain over multiple selection cycles can be corrected by refreshing the data used to train the model. This process can use data from concurrent evaluation of progeny and new genetic sources in an ongoing breeding programme (Li & Brummer 2012; Esfandyari *et al.*, 2020). The simulation used a GS prediction accuracy of 0.26, which limited response to selection. While this rate was reasonable as a basis for simulation, given prediction accuracy was positively correlated with the rate of gain, increasing the size of the reference population to lift accuracy may offer another way to improve ΔG per cycle (Faville *et al.*, 2018). Potential ΔG increases with numbers of selection candidates (Jahufer *et al.*, 2021), which suggested that these results, based on 150 candidates per family, were on the lower end of potential ΔG per cycle, as there are often thousands of candidates per family. Overall, these findings emphasised the need to increase the size and scope of GS model training sets, to apply the GS model to higher numbers of selection candidates and to refresh the GS model at regular intervals to better realise the advantages of GS in a breeding programme (Esfandyari *et al.*, 2020; Jahufer *et al.*, 2021).

Critically, the simulations reported here did not account for the potential to increase the number of selection cycles per unit time, another factor that could contribute to increasing ΔG . For example, conventional genotypic selection cycles for PRG include field assessments which take 3–5 years to execute. GS allows a subsequent cycle to be completed within a year or less (Jighly *et al.*, 2019) as GEBVs can be estimated when

the selection candidates are seedlings. However, for this to be effective in accelerating a multi-trait breeding programme, a GS model needs to be effective for all essential traits required under selection in the breeding programme, as has recently been demonstrated in cereal breeding (Gill *et al.*, 2021). The longstanding issues of negatively correlated traits, genotype \times environment interactions, and the challenge whereby increasing the number of traits generally slows the rate of gain for the selection index are not directly overcome by GS. However, there are examples where secondary traits can be used to improve the accuracy of a GS model, which warrant further evaluation (Arojju *et al.*, 2020; Gill *et al.*, 2021).

Use of GS over multiple cycles resulted in increased inbreeding and diminishing response to selection (Figures 2 and 4). Weighting parent selection to account for relatedness (Lin *et al.*, 2017a) and re-combination among breeding populations can be used to slow inbreeding and sustain ΔG over time. This emphasised the value of having multiple breeding populations under selection in a GS breeding programme.

The issues of relatedness between the training set and the selection candidates need further research. This can be addressed by increasing the size and diversity of the reference population, and may be addressed by augmenting the model with other trait-based data sources, such as hyper-spectral reflectance to allow model accuracy to be maintained among less-related selection candidates (Galán *et al.*, 2021), or by using trait-assisted GS (Arojju *et al.*, 2020).

Looking ahead, more research is needed to prioritise and optimise responses in relation to multi-trait indices, incorporating environmental performance and climate adaptation traits. This will forecast their genetic and economic impact, help optimise logistics of breeding method integration and provide value chain analysis in relation to economic impact.

In conclusion, a simulation-based analysis of small-scale implementation of GS in perennial ryegrass breeding indicates this scale is viable but not optimal, and revealed factors influencing genetic gain and cost-efficiency outcomes. These findings were broadly consistent with other simulation-based studies, and with emerging empirical evidence from progeny evaluation in field trials. Using a combination of simulation approaches can enable decision support for GS technology integration for long-term forage breeding programmes to sustainably deliver cost-effective genetic and economic gains.

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