





ADVANCES IN MINING RESTORATION

RESEARCH ARTICLE

Seed quality and the true price of native seed for mine site restoration

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Native seed underpins the success of most terrestrial restoration efforts globally; however, the fragility of the native seed supply chain presents a key challenge to achieving global restoration goals. With the current heightened global focus on ecological restoration, seed supply chains are under unprecedented pressure worldwide. New and practical solutions are required to help the native seed industry move toward more sustainable and reliable supply, and in turn, facilitate more cost-effective, successful, seed-based restoration. Here we focus on species used in biodiverse mine site restoration in two regions of Western Australia as a test case for evaluating two key elements of the seed supply chain: seed quality and price. The study assessed seed quality in 185 species, then combined these results with seed price to determine the actual cost of pure live seeds (PLS) used in restoration. Average seed quality, expressed as a weight percentage of PLS, is 55%. The average price for a native seed batch across 129 species is \$1,093 Australian dollars (AUD)/kg, and when adjusted for viability and purity is \$2,600 (AUD)/ kg of PLS. We suggest replacing the traditional approach of pricing seed per unit weight (\$/kg) with a new method that would reflect seed quality and unit number; price per thousand pure live seeds (\$ TPLS). We posit that this new way of pricing native seeds would increase transparency and information flow in the marketing of native seeds, which will, in turn, enable seed users to more reliably plan for, and evaluate the cost-effectiveness of seed-based restoration projects.

Key words: native seed supply chain, pure live seed, seed-based restoration, seed quality

Implications for Practice

- Systematic testing of native seed batches provides vital information to seed suppliers and users for optimizing seed sourcing (production and collection) and establishing quality-driven seed pricing.
- When viability is considered, the price of native seed per kilogram of pure live seeds is considerably higher than the unrefined price.
- Seed size and quality are usually not considered in the current seed pricing framework based on price per unit weight.
- Price per thousand pure live seeds includes both unit number and quality in a single easy to compare value, making seed pricing more transparent, and facilitating accurate budgeting, seed mix preparation, seed delivery, and reliable estimates of seed success in restoration.

efforts globally (Pedrini et al. 2020). However, the fragility of the native seed supply chain presents a key challenge to achieving global restoration goals (National Academies of Sciences, Engineering 2020). The UN Decade on Ecosystem Restoration, combined with the ambitious goal of the Bonn Challenge to restore 350 million hectares of degraded land back to sustainable, resilient ecosystems worldwide by 2030 (IUCN 2020), will see a significant increase in demand for native seed in the coming years—with around 1,750 million tons of native seed required to achieve these restoration goals (based on a seeding rate of 5 kg seed/ha; Merritt & Dixon 2011).

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Introduction

The UN Decade on Ecosystem Restoration 2021–2030 aims to prevent, halt, and reverse the degradation of ecosystems worldwide (United Nations 2021) and raises global expectations for the successful re-establishment of ecosystems that have been damaged, degraded, or destroyed (Young & Schwartz 2019). Native seed underpins the success of most terrestrial restoration

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As one of the most damaged and biodiverse continents, Australia is initiating more ecological restoration projects than ever before (McDonald & Clarkson 2020). The new and ever-expanding industry of carbon offset planting (Standish & Prober 2020) combined with existing industries such as post-mining restoration (Erickson et al. 2017) means that demand for native seed is rapidly increasing. However, native seed used in Australian restoration activities is almost entirely wild-harvested (Broadhurst et al. 2017; Hancock et al. 2020) leading to concerns for the sustainability, robustness, and reliability of the Australian native seed supply chain to deliver restoration outcomes (Mortlock 2000; Broadhurst et al. 2008). Thus, to ensure that the native seed supply chain is robust and capable of supporting large-scale ecosystem restoration, it is critical to improve current practices in the native seed and restoration industries and to focus research strategies to address the practical issues faced by the native seed sector.

Limited Availability of Native Seed

A major bottleneck in the native seed supply chain is the limited availability of seeds in terms of quantity and diversity of species of appropriate origin (Merritt & Dixon 2011). Factors contributing to the deficit in seed include: seasonality, over-reliance on wild-harvested seed, lack of knowledge and expertise required to undertake seed collections, habitat fragmentation, the ongoing decline of native vegetation communities, and the need to spread collections spatially and temporally (Gibson-Roy et al. 2021). In Australia, these factors are compounded by the high level of biodiversity and endemism and the large number of species with narrow ranges and distinctive genotypes (Hopper & Gioia 2004; Breed et al. 2013).

In ecological restoration, native seed should be collected following practices that ensure representation of a population's genetic diversity while also maintaining the reproductive capability of the donor population (Pedrini et al. 2020). As such, many species, especially those that are threatened, rare, or have a limited or fragmented distribution, must be collected over multiple seasons to ensure that sufficient volumes of seed are obtained without damaging the natural populations (Broadhurst et al. 2015).

Collection of seeds from wild populations requires specialist knowledge of the target species and donor population. Developing a sound understanding of the phenology of hundreds of species and the ability to correctly interpret seasonal variation, climatic conditions, and numerous other variables (e.g. pollinators, seed predators) requires appropriate training and years of on-ground experience to obtain seeds at the optimal collection time (Ritchie et al. 2017). Unfortunately, increased demand for native seed is not being met with an equivalent increase in recruitment and training of new seed collectors, placing the burden of supply on a limited and aging group of collectors that possess the necessary experience and knowledge (Broadhurst et al. 2015).

High Cost of Native Seed

Difficulty in procurement and limited availability are the major factors contributing to the high cost of native seeds, with rising demand and low supply escalating prices. Prices are further

exacerbated by fluctuations in seed demand, with purchase of seed often coinciding with increased restoration activity, funding availability, or approaching deadlines such as mine closure (Erickson & Halford 2020). At times, limited foresight and planning result in seed collection activities being relegated to a few years prior to the commencement of restoration works. For multi-decade mining operations with large seed demands, this is clearly inadequate (Erickson et al. 2017). This poor planning then places pressure on seed collectors and donor populations which the native seed industry in its current state is not able to accommodate (Hancock et al. 2020). Moreover, relatively little information on the price of supplied seeds per wild species has been reported in the literature, with the most reliable estimate at $\$749 \pm 65/\text{kg}$ based on 88 species used for mine site restoration in the Pilbara region of Western Australia (Merritt & Dixon 2011). Note that all prices presented in this paper are in Australian dollars (AUD), and when different currencies are used (e.g. USD) this is specified.

Lack of Application of Quality Testing

Australian native seeds are inherently challenging to handle and germinate due to the high level of taxonomic diversity and resultant wide range of seed morphological and physiological features (Erickson et al. 2016). As such, there is no standard method for ensuring the quality of native seed lots (Frischie et al. 2020). While protocols for testing the quality of agricultural seeds have long existed, often, these cannot be easily adapted to native seeds. Agricultural seeds have been rigorously selected over centuries for consistent seed traits and are produced *en masse* to ensure homogeneity within and between seed batches to deliver a uniform crop (International Seed Testing Association 2020). However, resilient, robust, ecological restoration relies on high biodiversity and genetic diversity, and as such requires relatively small quantities of genetically diverse seed of many different species with widely differing morphology and germination requirements (Erickson & Halford 2020). Thus, creating protocols for testing native seeds in such biodiverse restoration programs is a complex and often costly endeavor (Hancock et al. 2020).

Recently, the International Network for Seed-Based Restoration (INSR) developed the first *International principles and standards for native seeds in ecological restoration* providing seed suppliers and users with a common framework, terminologies, and clear guidelines outlining native seed testing approaches that underpin effective management of the native seed supply chain (Cross et al. 2020; Pedrini & Dixon 2020). However, the Australian native seed industry is yet to widely implement such methodologies, with most native seed lots in Australia supplied without critical seed quality information (Hancock et al. 2020). This issue is not uniquely Australian with most countries (with the exception of the United States and a few European countries) having limited native seed quality testing requirement and capability (Marin et al. 2017).

Aims and Objectives

Here we address some of the key deficiencies in the Australian native seed supply chain and propose new and practical

solutions as a case study of how the INSR Standards (Pedrini & Dixon 2020) can enable the global native seed industry to move toward more sustainable and reliable seed supply, to underpin successful and cost-effective seed-based restoration. Specifically, we assess seed quality and price for a wide range of taxonomically diverse species used in mine site restoration in two biodiverse regions in south-western Australia (Swan Coastal Plain and Mid-West) in order to:

- (1) test the methodology outlined in the *International principles and standards for native seeds in ecological restoration* (Pedrini & Dixon 2020) for assessing seed quality and provide information on thousand seed weight, purity, and viability for each batch;
- (2) provide an updated estimate of Australian native seed price based on data obtained from commercial seed suppliers;
- (3) derive the actual price of native seeds when quality is taken into consideration (thus eliminating inert materials and non-viable seed from batch weight), by adjusting price per kilogram of seed (\$/kg) to price per kilogram of pure live seeds (\$/kg PLS);
- (4) outline a new approach for marketing native seeds that would reflect seed quality and unit number: price per thousand pure live seeds (\$/TPLS) instead of price per unit weight (\$/kg).

We posit that this new method of pricing native seed batches would increase information flow and transparency in the marketing of native seeds, which will in turn enable seed users to more reliably plan for, and evaluate the cost-effectiveness of, seed-based restoration projects.

Methods

Species Selection and Seed Sourcing

Native species commonly used in ecological restoration activities at two mine sites from two bioregions of Western Australia (WA) were selected for use in this study. One set of species is used in restoration at Karara Mining Limited's (KLM) iron ore mine located in the semiarid (approximately 300 mm annual rainfall) Mid-West Region (Yalgoo IBRA region) of WA, approximately 300 km north-east of Perth. The other is used at Hanson Australia's Gaskell Sand Plant, located in the temperate higher rainfall (approximately 750 mm annual rainfall) Swan Coastal Plain Region (Swan Coastal Plain IBRA region) of WA (Fig. 1A) approximately 30 km north of Perth. All seed lots used in this study were acquired directly from the mining company or purchased from commercial seed suppliers that supply both mining operations.

A total of 185 species were tested, 115 of which were from the Mid-West Region, and 70 from the Swan Coastal Plain Region (Fig. 1B). The life forms of species tested reflected those found in these communities with a predominance of shrubs (59%—110 species), followed by perennial forbs (17%—31 species), trees (14%—25 species), annuals forbs (6%—11 species), and grasses (4%—8 species) (Fig. 1C). Forbs are presented as perennial and annuals because such distinction has practical repercussions when evaluating species for potential seed production, as well as their use in broadacre restoration particularly for environments where rapid plant cover is required for soil stabilization/erosion control such as the post-mining environment. A total of 34 families were represented in this study with five accounting for over 55% of species diversity. The largest family was the Myrtaceae (representing 23% of species tested),

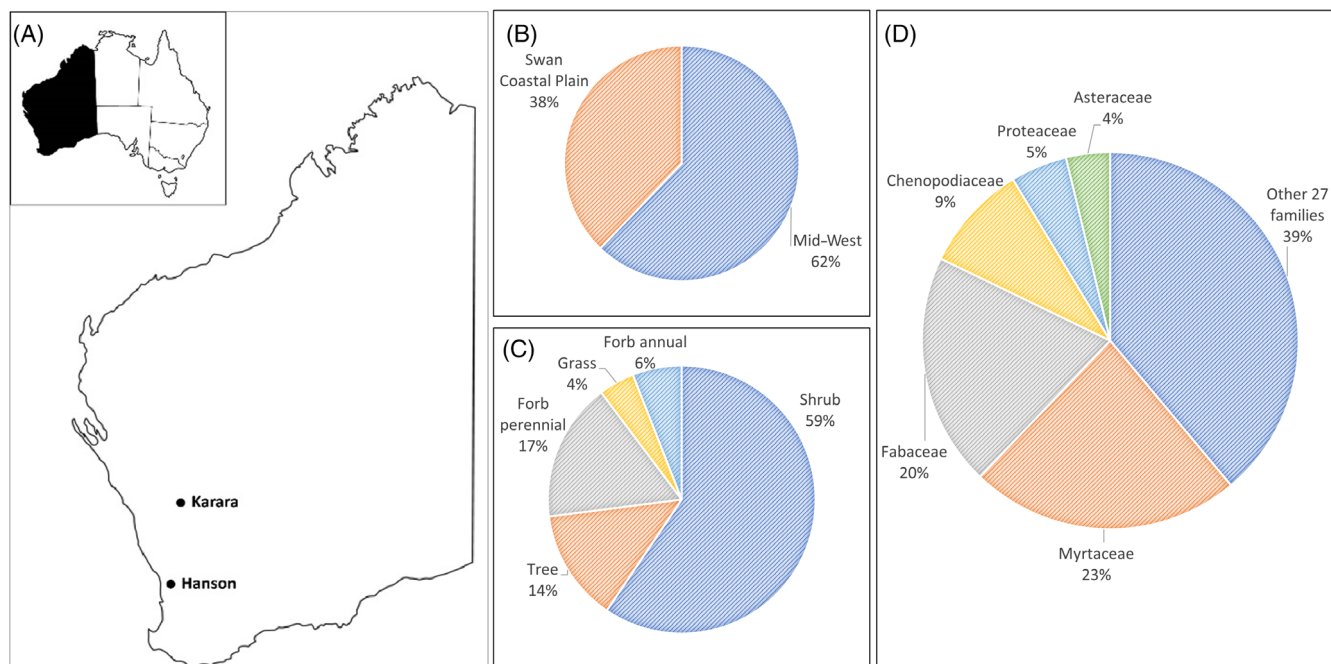


Figure 1. (A) Location of the study mine sites, Karara (Mid-West) and Hanson (Swan Coastal Plain), from which seed was sourced, within the southwest biodiversity hotspot of southwestern Australia. (B) Proportion of species studied that originate from the Swan Coastal Plain and Mid-West regions of Western Australia. (C) Proportion of different life form types among species studied. (D) Representation of different families among species studied.

followed by the Fabaceae (20%), Chenopodiaceae (9%), Proteaceae (5%), and Asteraceae (4%) with the remaining 27 families accounting for the residual species diversity (39%—72 species) (Fig. 1D). The complete list of species, families, and regions of origin is provided in Table S1.

Seed Quality Testing

Seed quality was tested for 185 species, following the protocols outlined in the *International principles and standards for native seeds in ecological restoration* (Pedrini & Dixon 2020) (hereafter referred to as “The Standards”). A

proforma, adapted from the “Seed Quality Test” section presented in The Standards, was used to guide the testing process and record data (Fig. 2D). Data collected on the proforma were then entered into a Microsoft Access database (Microsoft, U.S.A.).

Each seed batch was thoroughly mixed prior to sampling and small subsamples extracted from different locations within the seed bag to obtain a representative sample and account for potential variation within the batch (due to density separation) (Native Seed Quality Task Force 2011). Batch purity (percentage) was assessed by measuring the proportion by weight of pure seed units (PSU), inert material, and non-target seeds

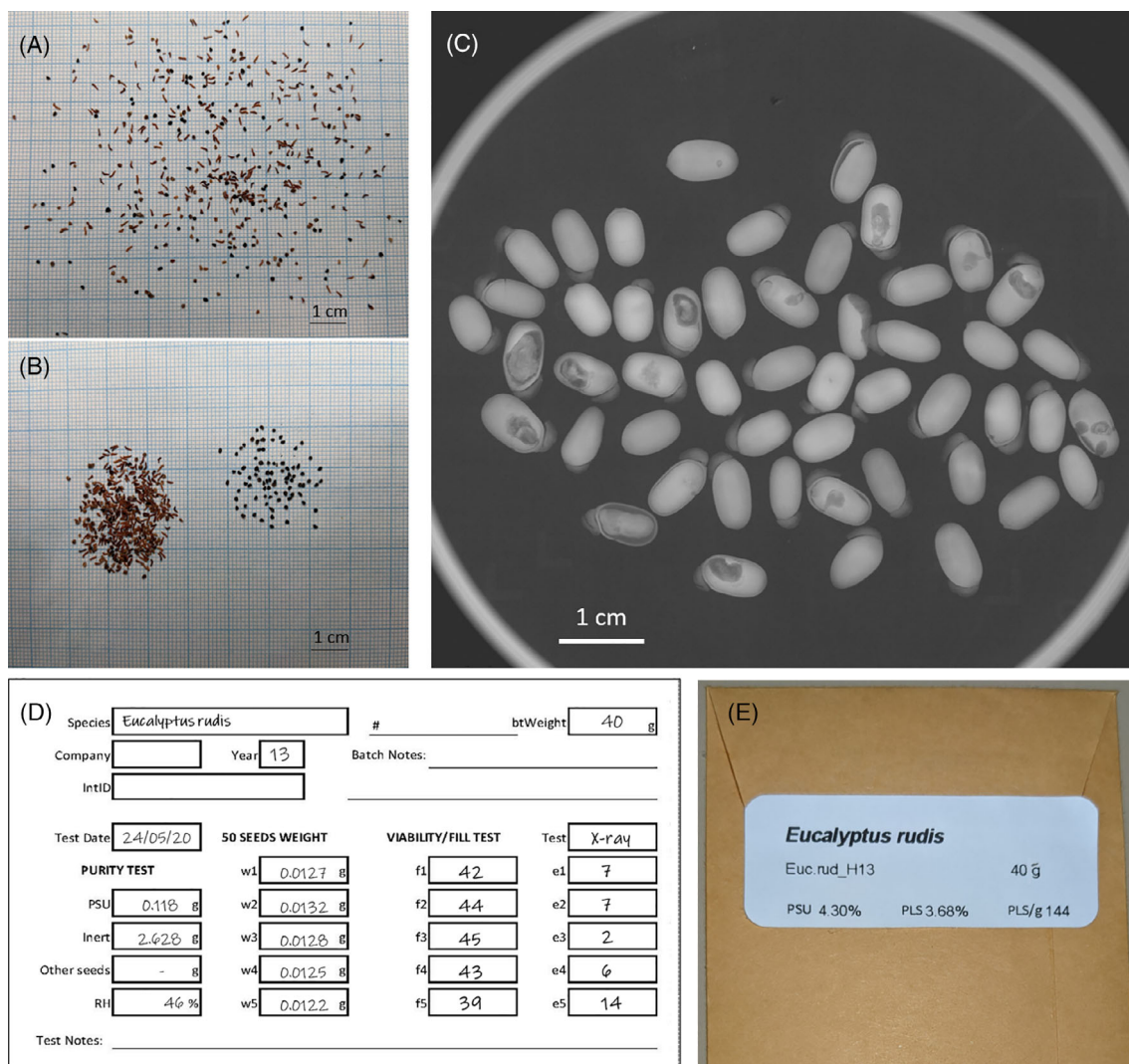


Figure 2. Purity and viability testing. (A) Subsample of *Eucalyptus rudis* as extracted from the seed batch, (B) separated fractions of non-seed material (left) and pure seed units (right) from the same subsample of *Eucalyptus rudis*. By weighing each fraction, it is possible to estimate the PSU%. (C) X-ray image of *Acacia saligna* where it is possible to differentiate between seeds that appear healthy to seeds that are shriveled or have evidence of predation. (D) Form used to collect data on seed quality. This form is a simplified version of the proforma presented in the International Principles and Standards for Native Seeds in Ecological Restoration. The viability/fill data are presented in rows 1–5, the number on the left (f) is the number of filled seeds, the one on the right (e) is the number of seed considered non-viable because empty, predated, broken, or shriveled. Totals and averages are automatically calculated in the database. In the test field, it is specified which viability test was performed (X-ray, cut test, germination). In this case, all of the tests performed done via X-ray. (E) Label printed from the seed quality database reporting the key results of the quality test: PSU% and PLS%.

within each sample (Fig. 2A & 2B). Five replicates of roughly fifty seeds each were extracted from the PSU fraction, weighed, and used to calculate the thousand pure seed unit weight (TPSU/g). The precise number of seeds of each replicate was determined when undertaking X-ray tests.

Viability testing was performed by subjecting the five subsamples used to calculate the TPSU weight to X-ray imaging (VersaVision Digital Specimen Radiography System, Faxitron, AZ, U.S.A.). The resulting images were then analyzed to determine the precise number of seeds, the proportion of seeds that appeared to be filled and the proportion that appeared to be damaged, predated, shriveled, or underdeveloped (Fig. 2C). The GNU Image Manipulation Program (GIMP, Version 2.10; GIMP Development Team 2019) was used to edit the images and mark potentially viable and non-viable seeds. For species where differences between viable and non-viable seeds were not clear, especially on Myrtaceae where seeds and ovulode appear very similar, a cut test or germination test was used to support the interpretation of X-ray images.

The result of the viability test was combined with the result of the purity test to calculate the percentage (by weight) of pure live seed (PLS) in the batch, as per the following equation:

$$\text{Pure live seed (\%)} = \frac{\text{Viable seeds (\%)} \times \text{pure seed units (\%)}}{100}$$

Seed Price Per Batch (\$/kg) and Adjustment for Viability (PLS \$/kg)

Price data in AUD were obtained from commercial seed suppliers for 147 of the 185 species tested for seed quality. Where prices were not provided in kilogram but were listed in lower units of measure (i.e. 1, 10, or 100 g), the quantity of seed sold at the lowest relative price was converted to price per kilogram. In cases where prices for the same species were available from multiple sources, the lowest price was used.

The price of each seed batch was then adjusted to consider viability (as obtained via quality testing) to determine the price per kilogram of pure live seeds by using the following formula:

$$\text{Price PLS (\$/kg)} = \frac{\text{Price seed batch (\$/kg)}}{\text{PLS (\%)}}$$

Very high prices per kilogram of some species (e.g. rare, difficult to collect, low demand, and small-seeded species) paired with very low viability resulted in several outliers. In extreme cases, this produced unreasonable results; for example, *Goodeinia cynopotamica* (syn *Velleia cynopotamica*), at a price of \$6,600/kg combined with a viability of 0.2% PLS, resulted in a price per kilogram of PLS of over \$4.5 million. The interquartile range method was employed to first identify then remove (19) outliers from the dataset, resulting in 128 species that were

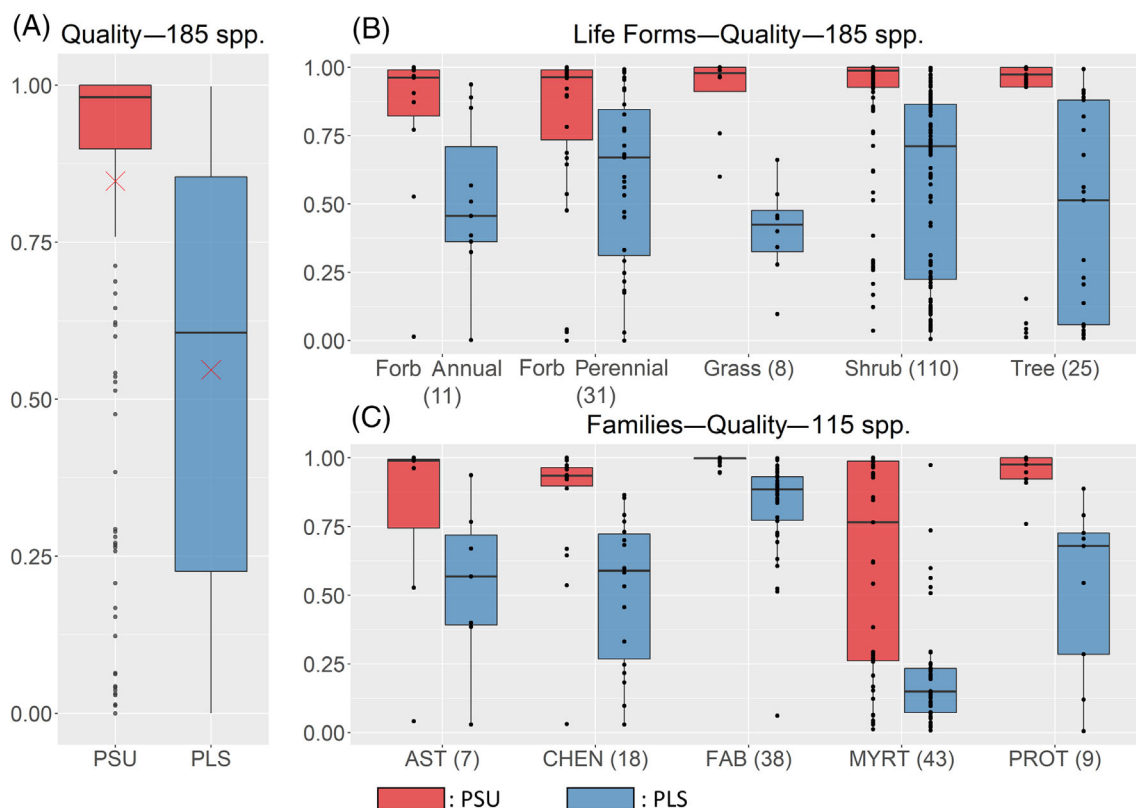


Figure 3. (A) Proportion of pure seed units (PSU) and pure live seeds (PLS) present in the seed batches of 185 Australian native species. (B) Proportion of PSU and PLS for 185 species divided according to life form (forb annual, forb perennial, grass, shrub, and tree). (C) Proportion of PSU and PLS for 115 species from five families. AST, Asteraceae; CHEN, Chenopodiaceae; FAB, Fabaceae; MYRT, Myrtaceae; PROT, Proteaceae.

then used for additional analysis. The complete list of 147 species and their calculated price of PLS (\$/kg) is provided in Table S1.

Price Per Thousand Pure Live Seeds

The above data were adjusted for seed weight to determine the \$ TPLS. The weight (g) of a TPLS was determined using the TPSU weight (obtained during purity testing outlined above) and the PLS percentage (obtained through viability testing outlined above), as per the following formula:

$$TPLS (g) = \frac{TPSU (g)}{PLS (\%)}$$

where a price per unit weight was known, it was converted to price per gram (\$/g), then the price per thousand pure live seeds (\$ TPLS) was calculated as follows:

$$\$ TPLS = TPLS (g) \times \text{price of seed batch } (\$/g)$$

As was the case when seed price was adjusted for viability, adjustment of seed price to TPLS (\$) presented several outliers. These outliers were removed using the interquartile range method (as previously described), which resulted in 129 species remaining in the dataset. It should be noted that some species present in the \$ TPLS dataset are not present in the \$/kg PLS

and vice versa. The complete list of 147 species and their calculated \$ TPLS is provided in Table S1.

Data Analysis and Interpretation

Results are presented as descriptive statistics indicating the mean, median, interquartile range, and outliers for all data subsets and variables assessed (PSU, PLS, \$/kg, PLS \$/kg, and \$ TPLS). Data analysis and visualization were conducted in RStudio, and figures were produced using the ggplot2 package (Wickham 2016).

Results

Seed Quality Testing

For all 191 Australian native species assessed, the proportion of PLS (filled seeds) was considerably lower than the proportion of PSU, with average PSU being $85 \pm 2\%$ and average PLS at $55 \pm 2\%$ (Fig. 3A). The distribution of PSU and PLS across all species was strongly asymmetric and skewed to the left (coefficient of skewness PSU: -1.9733 , PLS: -0.2759).

Across all life forms, PLS% was considerably lower than PSU% (Fig. 3B). Grass (8) species had the highest PSU ($91 \pm 5\%$), while tree (25) species had the lowest ($76 \pm 8\%$). PSU in a seed lot was not directly proportional to PLS. Perennial forb (31) and shrub (110) species had the highest PLS ($59 \pm 6\%$

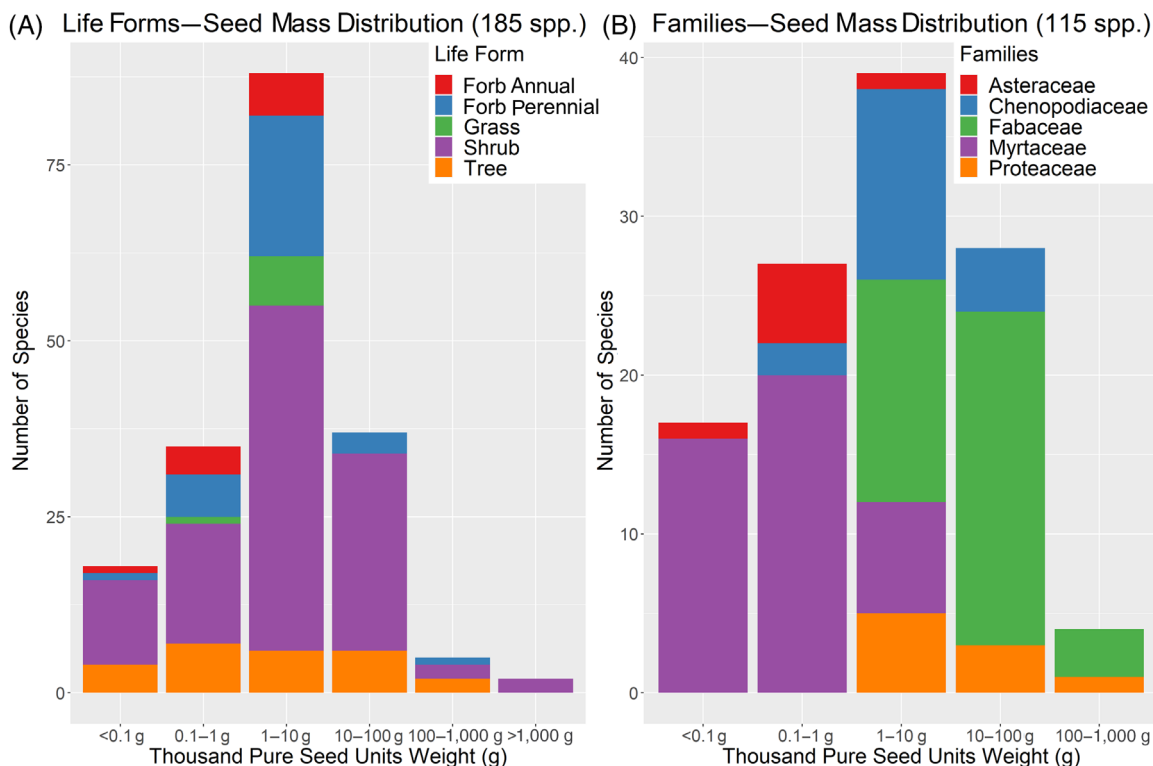


Figure 4. (A) Distribution of thousand pure seed unit weight (TPSU [g]) for 185 Australian native species assigned into one of five different life forms (forb annual, forb perennial, grass, shrub, and tree) used in this study. (B) Distribution of TPSU weight for 115 Australian native species from the five most speciose families (Asteraceae, Chenopodiaceae, Fabaceae, Myrtaceae, and Proteaceae) used in this study.

and $57 \pm 3\%$, respectively), while grass species had the lowest ($40 \pm 6\%$; Fig. 3B).

Seed quality of 115 species from the five most representative families, Asteraceae (7 species), Chenopodiaceae (18 species), Fabaceae (38 species), Myrtaceae (43 species), and Proteaceae (9 species), was analyzed. Fabaceae species had the highest purity ($99 \pm 0\%$), while Myrtaceae species had the lowest ($61 \pm 6\%$). As with the life forms, the PSU% in a seed lot was not directly proportional to the PLS% in a seed lot. Fabaceae species had the highest PLS% ($83 \pm 3\%$), and Myrtaceae species had the lowest ($21 \pm 3\%$; Fig. 3C). The seed quality results for life forms and families are reported in Table S2.

Seed Weight Distribution

Seed weights of species used in this study ranged from 0.009 g per TPSU (*Melaleuca preissiana*) to 3,238 g per TPSU (*Santalum spicatum*), with seeds for most species falling within the 1–10 g per thousand seeds weight range (Fig. 4).

Seeds of annual forbs and grasses were the smallest across life forms, ranging from <0.1 to 10 g per TPSU. PSU of perennial forbs and trees followed a roughly bell-shaped distribution across the <0.1–1,000 g weight ranges, while TPSU of shrubs spanned the entire weight spectrum (Fig. 4A).

PSU of the families Myrtaceae and Asteraceae were the smallest, ranging from <0.1 to 10 g per TPSU, while seeds from the

Fabaceae and Proteaceae were the largest, ranging from 1 to 1,000 g per TPSU (Fig. 4B).

Seed Price for Batch and Adjusted for Viability

Across all 128 Australian native species assessed for seed price (19 outliers removed—see Table S1), the price per kilogram of PLS was over double the price per kilogram of raw seed lots, with the mean price per seed batch being $1,093 \pm 146$ \$/kg and the mean price of PLS being $2,600 \pm 278$ \$/kg (Fig. 5A). The distribution of batch \$/kg and PLS \$/kg across all species was strongly asymmetric and skewed to the right (coefficient of skewness for batch \$/kg: 3.1350, PLS \$/kg: 1.6587).

Perennial forb (17) species had the highest price per kilogram of seed ($\$2,067 \pm 663$), while tree (20) species had the lowest price per kilogram of seed ($\$568 \pm 109$). Grass (6) species had the highest price per kilogram of PLS ($\$3,899 \pm 1,163$), while shrub (79) and tree species had the lowest price per kilogram of PLS ($\$2,490 \pm 371$ and $\$2,439 \pm 593$, respectively; Fig. 5B).

The five most represented families in the price dataset encompass a total of 91 species: Asteraceae (5 species), Chenopodiaceae (16 species), Fabaceae (33 species), Myrtaceae (32 species), and Proteaceae (5 species). Proteaceae species had the highest price per kilogram of seed ($\$2,600 \pm 1,340$), while Fabaceae and Chenopodiaceae species had the lowest ($\$429 \pm 67$ and $\$461 \pm 239$, respectively). Myrtaceae species had the highest price per

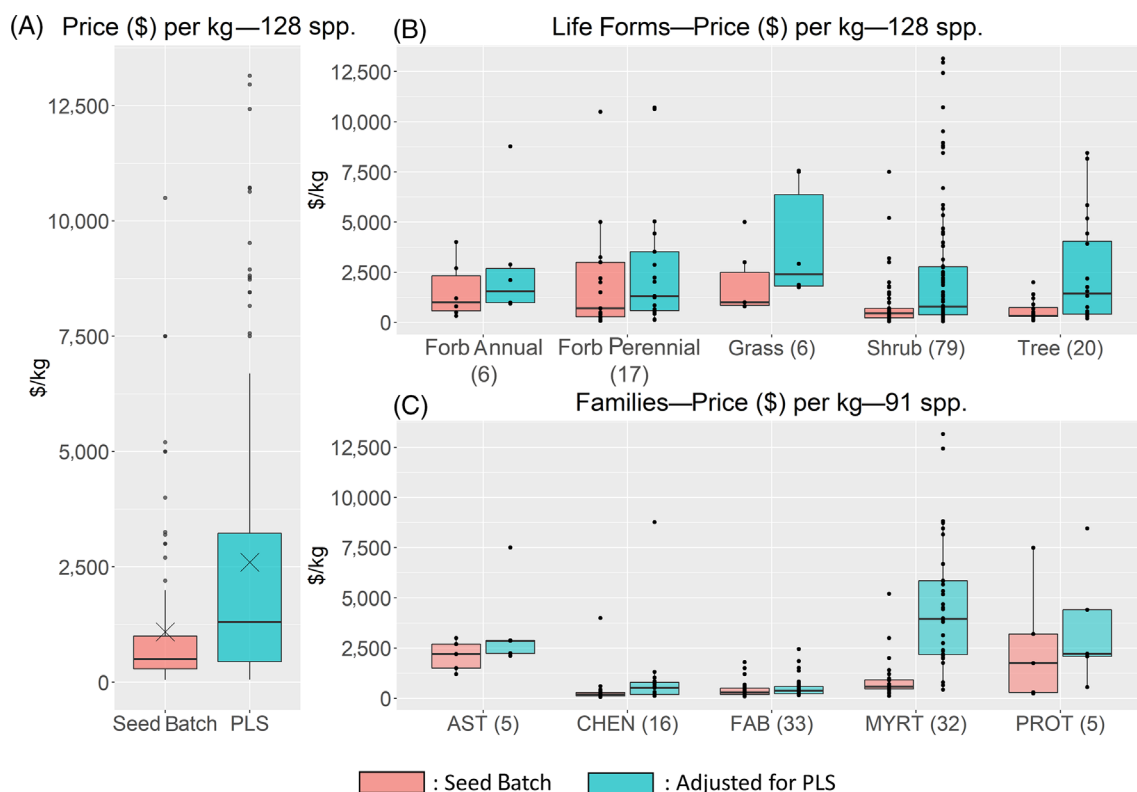


Figure 5. Price per kilogram of seed batches (pink) and adjusted for viability: PLS (blue) of (A) 128 Australian native species, (B) for 128 species divided according to life form (forb annual, forb perennial, grass, shrub, or tree), (C) for 91 species from five families. AST, Asteraceae; CHEN, Chenopodiaceae; FAB, Fabaceae; MYRT, Myrtaceae; PROT, Proteaceae.

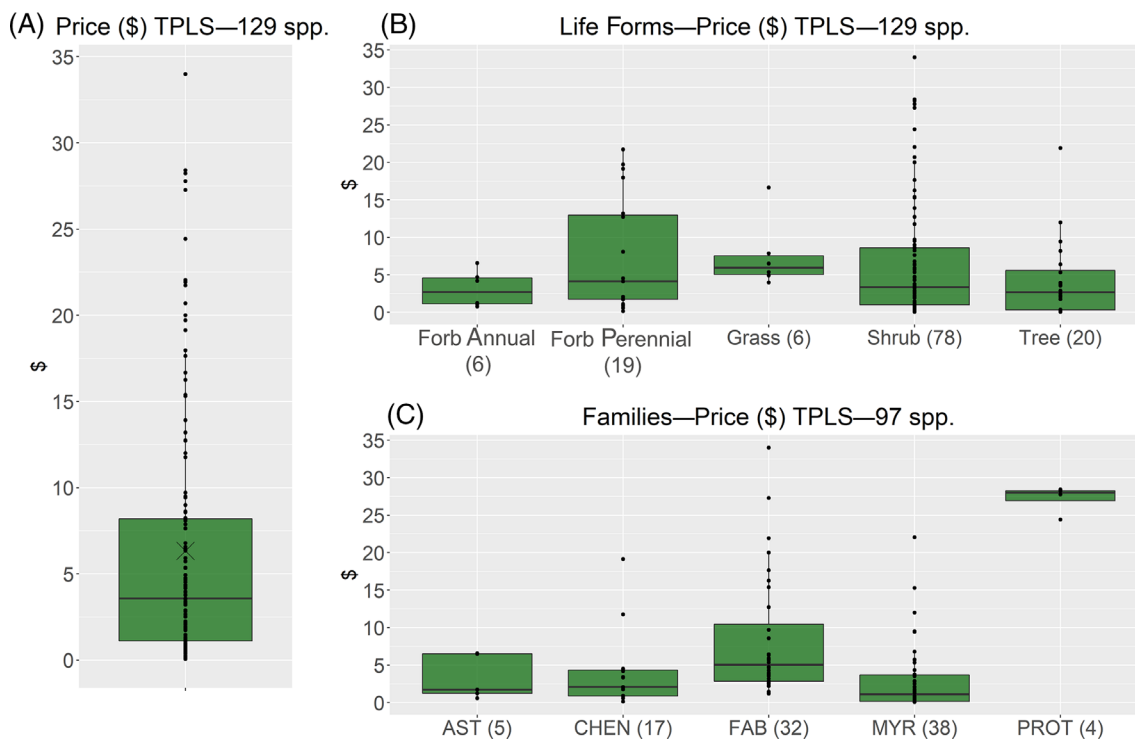


Figure 6. (A) Price per thousand pure live seeds (\$ TPLS) for 129 Australian native species. (B) Price per TPLS for 129 species by life form (forb annual, forb perennial, grass, shrubs, and tree). (C) Price per TPLS for 97 species for five families. AST, Asteraceae; CHEN, Chenopodiaceae; FAB, Fabaceae; MYRT, Myrtaceae; PROT, Proteaceae.

kilogram of PLS ($\$4,582 \pm 564$), while Fabaceae species had the lowest ($\$560 \pm 91$; Fig. 5C). The seed price results for life forms and families are reported in Table S3.

Seed Price Per Thousand Pure Live Seeds

The mean \$ TPLS of 129 Australian native species was $\$6.34 \pm 0.66$ (Fig. 6A). The distribution of \$ TPLS across all species was strongly asymmetric and skewed to the right (coefficient of skewness: 1.6507).

In terms of life forms, annual species had the lowest mean price per TPLS ($\$3.10 \pm 0.98$), while perennial forb and grass species had the highest mean price per TPLS ($\$7.26 \pm 1.73$ and $\$7.55 \pm 1.90$, respectively; Fig. 6A). In comparison, the price of trees and shrubs was between these three life form groups (Fig. 6). When the price of the five largest families was assessed, the Asteraceae and Chenopodiaceae species had the lowest mean price per TPLS ($\$3.32 \pm 1.32$ and $\$3.78 \pm 1.17$, respectively), while Proteaceae species had the highest mean price per TPLS ($\$27.21 \pm 0.94$). The price per TPLS for life forms and families are reported in Table S4.

Discussion

Seed Quality

Assessment of seed quality provides critical information to seed collectors, suppliers, and end-users that has major implications

for budgeting, planning, and ultimately the level of success for any restoration project (Erickson & Halford 2020; Frischie et al. 2020). However, at present, the reporting of seed quality is not a standard procedure for most native seed suppliers due to the time, costs, and lack of skilled staff to undertake these critical assessments, which is compounded by end seed users being generally unaware of the critical need for seed quality estimations (Hancock et al. 2020; Pedrini & Dixon 2020). In Western Australia, the Revegetation Industry Association (RIAWA) has developed local standards for harvesting, processing, storing, and marketing native seeds (RIAWA 2019a), raising the bar for commercial seed collection and sales practices. However, according to the RIAWA standards for seed quality testing, just two of the five quality grades require viability testing (“Conservation” and “A+”), while for lower grades (“A” and “B”) only purity testing is needed, and for the lowest grade (“C”), no testing is required whatsoever (RIAWA 2019b). This study shows that the purity of seed batches is, on average, high (85% PSU), with batches containing a high proportion of PSU versus inert material. However, there were exceptions in some families such as the Myrtaceae due to high ovulode amounts present in batches (Bohte & Drinnan 2005). The purity test is a rapid and straightforward assessment; however, our results show that this test alone greatly overestimates actual seed quality. Moreover, for species where it is difficult to differentiate seeds from ovulodes of similar color, shape, and size the results of purity test (when replicated within the same batch) could be highly variable due to inconsistency in assessment. If quality assessment for

such species is limited to the result of purity test (PSU%), it would be unreliable. However, potential errors in interpretation during the purity test are generally corrected by the viability test (VSU%), where better identification between seeds and ovulodes is possible, allowing for a more consistent and less variable PLS (e.g. if a batch of *Eucalyptus* sp. is assessed for PSU at 20% and then the PSU fraction is tested via X-ray imaging, returning a 50% VSU, the resulting PLS would be 10%. The same batch is then examined by someone else who estimate the PSU at 50%. However, when it is tested on the X-ray the result would be 20% VSU, returning the same PLS of 10%).

The average PLS across all seed batches was $55 \pm 2\%$, with critical life forms such as grasses (PLS $40 \pm 6\%$) and families like Myrtaceae (PLS $21 \pm 3\%$) having most of the batch weight composed of non-viable seeds and other inert material. Higher quality seed batches could be achieved by improving seed cleaning and sorting procedures, thus ensuring that most non-seed material and non-viable seeds are removed from the batch (Erickson et al. 2016; Frischie et al. 2020; Errington et al. 2021). The combination of seed purity and viability testing can provide a generally reliable estimation of seed quality (Pedrini & Dixon 2020); however, some limitations remain with the methods used in this study that need to be considered.

Viability testing based on visual assessment via X-ray imaging (and similarly cut tests) can overestimate seed batch quality as seeds that appear filled and healthy may not actually be alive due to either poor storage conditions, disease, or genetic factors (Mohamed-Yasseen et al. 1994; Faast et al. 2011; Merritt et al. 2021). The tetrazolium test can provide a more accurate assessment of seed viability based on direct metabolic activity within the seed embryo (Marin et al. 2017); however, it is destructive, laborious, and time-consuming, and protocols for the accurate performance of the test (i.e. imbibition time, temperature, cut orientation) and interpretation of results (i.e. stain pattern) must be understood (International Seed Testing Association 2020) with many species showing inconsistent staining patterns that are hard to accurately decipher, particularly for Australian native species (Paynter & Dixon 1990; Ooi et al. 2004).

Another method for assessing seed batch quality is through germination tests, which is often considered the most reliable means to assess seed viability as seeds that germinate are clearly alive (Pedrini & Dixon 2020). However, if most seeds are filled but show low germination it may be necessary to undertake additional assessments to determine if a lack of germination is due to low viability (via tetrazolium test), poorly resolved germination requirements (i.e. temperature, light, stimulants; Merritt et al. 2007) or the presence of complex seed dormancy, which is widespread and often not fully understood for native seed (Kildisheva et al. 2020).

Ultimately, what makes a native seed testing regime practical for frequent use comes down to a trade-off between accuracy, practicality, and economic feasibility. The costs of seed quality testing could be reduced by centralizing testing facilities and using robust testing methods calibrated to individual native species, similarly to what ISTA accredited testing centres already do for crop varieties. Further improvement could be achieved

by automating and streamlining the process through the adoption and integration of innovative technologies such as advanced imaging systems and machine learning (Nansen et al. 2015; Colmer et al. 2020). For these reasons, the combination of X-ray imaging with purpose-built software for assisted image interpretation is a promising technology for faster and cheaper viability assessment (de Medeiros et al. 2020). Precision can be improved through careful calibration for each taxon, by adjusting the X-ray imaging results to germination outcomes and dormancy assessments (Ahmed et al. 2018). Once sufficient images with accurate viability interpretation are obtained, machine learning could be deployed to perform the analysis and automate the process across a broad range of morphologically distinct and taxonomically diverse species (Al-Turki & Baskin 2017).

However, regardless of the method employed, it is important to seed users that seed suppliers understand and communicate seed viability.

Seed Price

The average native seed price of $\$1,093 \pm 149/\text{kg}$ reported in this study is higher than the average price of $\$749 \pm 65/\text{kg}$ reported a decade ago by Merritt and Dixon (2011), even when this price is adjusted to $\$875 \pm 76/\text{kg}$ to account for inflation over the last decade (Reserve Bank of Australia 2021). While these average seed prices are not directly comparable due to being obtained from different species pools and regions, different regulatory environments, and changing market demands, both values sit within a similar range, roughly around the $\$1,000/\text{kg}$ mark, and provide a general indication of how expensive native seeds can be for restoration in Australia. However, when adjusted for viability, the recorded seed price per kilogram is almost 2.5 times higher than the current value, averaging $\$2,560 \pm 273/\text{kg}$ of PLS.

A particularly insightful piece of information obtained from seed batch prices is that the cost per kilogram of shrub (916 \$/kg) and tree (568 \$/kg) seed is substantially lower than that of understory species (grasses: 1,587 \$/kg, perennial forbs: 2,067 \$/kg, annual forbs: 1,587 \$/kg). This discrepancy could be partially explained by the relative ease of identification, localization, and bulk collection of overstory species, though could also be attributed to the higher demand for trees and shrubs driven by the rapid surge in carbon sequestration planting initiatives where the focus is on easy to grow, rapidly maturing, and readily available shrubs and trees (Department of Primary Industries and Regional Development 2021). Higher demand for tree and shrub seeds has compelled seed collectors and suppliers to prioritize the sourcing of overstory species, improving collection efficiency by virtue of practical experience and better understanding of population phenology, ecology, and location, while understory species where much of the biodiversity and functional capacity of an ecosystem reside (Landuyt et al. 2019) are often overlooked.

However, despite the lower price per kilogram of shrub and tree seeds, when adjusted for viability, seed price (approximately 2,500 \$/kg) is not dissimilar from that of annuals and perennial forbs (approximately 2,770 \$/kg). This is due to the

presence of species of *Eucalyptus* and *Melaleuca* (Myrtaceae) among the overstorey life forms. It is common for Myrtaceae species to exhibit low intrinsic batch quality (21%) resulting from the abundance of non-seed material that is similar in size, shape, color, and density to viable seeds (Sweedman & Merritt 2006). This factor, combined with the relatively small size of Myrtaceae seeds, makes it difficult or commercially unfeasible to clean seed batches to a high purity.

Overall, this study highlights how costly Australian native seeds can be, especially when compared to the price of native seeds in other countries, where a different combination of factors influences seed cost. For example, the average price of native seeds used in restoration of the Colorado Plateau in the United States is 7.81 USD \$/lb (22.91 AUD \$/kg) (Camhi et al. 2019). This lower price in the United States could be attributed to a more developed native seed market, heavier reliance on seed production, and use of mostly herbaceous species (Phillips-Mao et al. 2015; Strehlow et al. 2017; Gibson-Roy 2018). Use of seed farming has the potential to substantially reduce the cost of native seeds (Pedrini et al. 2020; Zinnen et al. 2021). This approach may not be economically viable in the short term (i.e. <24 months) for slower-growing woody perennial species (Willyams 2015; Gibson-Roy et al. 2021), but may improve the availability and affordability of currently under-represented and expensive annuals and herbaceous perennials, and small shrubs (Gibson-Roy et al. 2021). The price of native seeds obtained from a community based native seed supply in Brazil ranges from USD \$1 to \$110/kg (1.33–146.66 AUD \$/kg) with half of the 130 species reported as being sold at less than USD \$15/kg (\$20.85 AUD \$/kg) (Schmidt et al. 2019). Similar to Australia, seeds in Brazil are mainly collected from natural populations; therefore, the lower prices could be attributed to other factors such as lower labor costs and the relatively large seed size of many tropical forest species (Pereira De Souza & Valio 2001). Seed size greatly affects the price on a per weight basis but is often overlooked and not considered in the sale of seeds.

Price Per Thousand Pure Live Seeds

The current system of selling native seeds at a price per weight assumes that a seed buyer is aware of differences in seed size, shape, morphology, and weight (across all of the species) and able to include these factors into calculations of seed requirements. Additionally, a lack of quality testing by the supplier leaves the onus for assessing viability on the end seed user, so by and large there is no obligation for seed suppliers to guarantee the quality of their product or at the very least provide basic seed quality information for each batch sold (Hancock et al. 2020). Though theoretically possible, it is not reasonable to expect restoration practitioners, mine site rehabilitation operators, or “carbon farmers” to have the facilities, expertise, and time to perform such tests. Instead, seed quality should be assessed by an independent seed testing laboratory, familiar with native seeds or, if such a facility is not available, by the seed supplier themselves (Pedrini & Dixon 2020).

The practice of pricing seeds on a weight basis reduces the motivation for suppliers to improve the purity/viability of a seed

batch by undertaking accurate seed testing, removing non seed material, and drying the seed appropriately (i.e. remove moisture, which therefore reduces seed weight) to ensure viability in storage. If the primary motivation of a seed customer is to seek the lowest price per kilogram rather than to secure a high-quality product, a seed supplier that cleans, dries, and tests their seeds and builds those costs into the final sale price would be at a commercial disadvantage against a competitor that supplies cheaper seeds at a (unknown) lower quality. Consequently, the effect of such a system distorts the original motivation for the supply of native seeds; that is to provide germination ready seeds to undertake environmental repair, which means that best practices are not established at the outset, ultimately being to the detriment of restoration outcomes.

Providing a \$ TPLS instead of per weight unit affords several advantages to seed users as both unit number (seed size) and quality are incorporated into a single easy-to-understand value. In addition, this approach allows the actual price of seeds to be determined more accurately and fairly and adds a level of transparency for seed users to directly compare the costs associated with the supply of species from different seed merchants. For example, in the Fabaceae, the batch price ($\$429 \pm 67$) and PLS price ($\560 ± 91) are much lower than that of any other family. However, because of the larger seed size, the price per TPLS in Fabaceae is $\$8.34 \pm 1.44$, which is more than double the price of small-seeded (and low quality) Myrtaceae ($\$4.01 \pm 1.14$), and higher than the average price per TPLS across all species ($\$6.34 \pm 0.66$). For expensive, rare, and relatively large seeds (e.g. *Banksia* spp.), the price is sometimes presented on a “cost per seed” basis (Commander et al. 2021). However, for most species the cost of a single viable seed will be less than a \$0.01. Using \$ TPLS instead would allow to work with more meaningful numbers.

Ultimately, the outcome of any seed-based restoration project will be measured by the diversity and number of plants successfully established, not simply by the quantity (kg) of seed sown. Having known and verifiable values of PLS for each batch supplied would make budgeting for seeding operations and preparation of seed mixes far easier and provide restoration practitioners with better tools to budget a restoration program more accurately. Moreover, precise estimates of how many PLS have been delivered to site would improve reliability and robustness of seeding success assessments during monitoring and allow better comparisons across sites, vegetation communities, seasons, and sowing conditions.

Moving away from the current seed pricing structure based on price-per-weight and adopting a new method of pricing native seeds based on TPLS would be a significant step toward the long-term sustainability of the industry, increased transparency in supply, and ultimately improving overall seed use efficiency with clear benefits to both seed suppliers and end seed users.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Data on seed quality, price, and \$ TPLS for all species.

Table S2. Summary statistics of seed quality data.

Table S3. Summary statistics of seed price data.

Table S4. Summary statistics of the price of a thousand pure live seed (\$ TPLS).

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