Building a botanical foundation for perennial agriculture: Global inventory of wild, perennial herbaceous Fabaceae species

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Summary

- Concerns about soil health and stability are focusing attention on crops that deliver both agricultural products and ecological services. Deep rooted, perennial plants that build soil organic matter, support diverse below-ground microbial communities, and produce edible seeds are key components underpinning ecological intensification; however few perennial, herbaceous crops have been domesticated for food.
- To facilitate development of edible, perennial, herbaceous crops, including perennial grains, we constructed an online resource of wild, perennial, herbaceous species - the Perennial Agriculture Project Global Inventory (PAPGI; http://www.tropicos.org/Project/PAPGI). The first component of this project focuses on wild, perennial, herbaceous Fabaceae species. We extracted taxonomic names and descriptors from the International Legume Database and Information Service. Names were added to PAPGI, a special project within the botanical database TROPICOS, where they link to specimen records and ethnobotanical and toxicological data. PAPGI includes 6,644 perennial, herbaceous Fabaceae species. We built a searchable database of more than 60 agriculturally important traits. Here we highlight food and forage uses for 314 legume species, and toxicological data for 278 species.
- The novel contribution of PAPGI is its focus on wild, perennial herbaceous species that generally have not entered the domestication process but that hold promise for development as perennial food crops. By extracting botanical information relevant for agriculture we provide a dynamic resource for breeders and plant scientists working to advance ecological intensification of agriculture, and for conservation managers working to preserve wild species of potential agricultural importance.

KEYWORDS

Ecological intensification, ethnobotany, Fabaceae, perennial grains, perennial polyculture, sustainable agriculture, toxicology.

Societal Impact Statement

Agroecosystems are constantly evolving to meet the needs of a growing population in a sustainable manner. Perennial, herbaceous crops deliver both agricultural products and ecological services. Until recently, edible, perennial, herbaceous crops, including perennial grains, were absent from agriculture. Perennial, herbaceous crops can be developed through wide hybridization between annual crops and perennial relatives or by de novo domestication of wild species. The diversity of wild, perennial, herbaceous legume species documented by the PAPGI increases resources available to breeders of perennial, herbaceous legumes, and raises awareness about previously untapped wild plant diversity in future crop development.

Introduction

Agriculture is the world's largest and most rapidly expanding ecosystem and the leading cause of biodiversity loss (Millennium Ecosystem Assessment, 2005). Agricultural intensification, increased productivity per unit area, results in dramatic yield gains through breeding and agronomic inputs (Mann, 1997), but also leads to soil degradation and erosion (Cox et al., 2006; FAO, 2009; Pretty, Toulmin, & Williams, 2011). Ecological intensification or multi-functional agriculture, an approach which aims to maximize agricultural products while simultaneously providing ecological services, is a compelling concept framing conversations about sustainable food production (Cassman, 1999; FAO, 2009; Doré et al., 2011; Bommarco, Kleijn, & Potts, 2013; Tittonell, 2014). Key components underpinning multi-functional agriculture are perennial, herbaceous crops; however, there are few perennial, herbaceous crops in large-scale production today.

High-yielding, deep rooted, perennial, herbaceous plants prevent erosion, build soil organic matter, support diverse below-ground microbial communities, provide ecosystem services, and produce seeds and biomass that can be harvested mechanically (e.g. Glover et al., 2010; Pimentel et al., 2012; Crews et al., 2016; DeHaan et al., 2016; Crews & Cattani, 2018). There are various ways in which perennial crops can be incorporated into agricultural systems, including rotation with annuals, in perennial monocrops, or in perennial polycultures (Cattani, 2014; Ryan et al., 2018). Although some perennial, herbaceous species are grown for biomass (e.g., alfalfa), here we turn our attention to perennial herbs grown for their edible reproductive structures, and focus in part on perennial grains (dry edible seeds harvested from perennial cereal, legume, oilseed, and pseudocereal crops; Van Tassel & DeHaan, 2013).

Despite their potential utility, wild, perennial, herbaceous species were rarely domesticated for seed or fruit production (DeHaan, Van Tassel, & Cox, 2005; Van Tassel, DeHaan, & Cox, 2010; Table S1). Several hypotheses have been proposed to explain the lack of perennial, herbaceous crops including trade-offs among vegetative and reproductive tissues and contingency effects of early agriculture which focused on annuals, among others (Van Tassel, DeHaan, & Cox, 2010). Today, perennial herbaceous crops are being developed through “wide hybridization,” where existing annual crops are crossed with perennial relatives, and *de novo* domestication of wild, perennial, herbaceous species (DeHaan & Van Tassel, 2014). Efforts to develop perennial grains are underway in several crop systems (Table 1); however, to our knowledge, there are few existing resources that provide information on wild, perennial, herbaceous plant biodiversity for the purposes of agricultural innovation.

The Missouri Botanical Garden (St. Louis, MO) is an exemplary leader in the field of plant biodiversity data and established the world’s first botanical database “Tropicos” (www.tropicos.org) to manage plant specimens and facilitate herbarium label production. Tropicos is unique because it is based on taxonomic names that link to herbarium specimens and other information, including other biodiversity information portals (Table S3). Here we report on the development of a special project within Tropicos, the Perennial Agriculture Project Global Inventory (PAPGI; http://www.tropicos.org/Project/PAPGI).

PAPGI represents a collaborative effort among botanists, evolutionary biologists, and breeders to inventory wild, perennial, herbaceous species and to provide relevant information needed to assess potential utility of previously undomesticated perennial species (Figure 1). This inventory is designed to answer fundamental questions such as: How many perennial, herbaceous species exist in agriculturally important plant families? Where are perennial, herbaceous species distributed geographically? What natural variation exists in agriculturally relevant plant traits?

Have perennial herbaceous species been used for food in the past and do they have any known toxic properties? In this first phase, we focus on the Fabaceae family (legumes). The specific objectives of this manuscript are to: 1) describe PAPGI construction; 2) introduce the Fabaceae inventory in PAPGI; and 3) highlight ethnobotanical and toxicological data for wild, perennial, herbaceous legumes.

Material and Methods

Acquisition of taxonomic, lifespan, and growth habit data. The legume family includes an estimated 20,856 species (Smýkal et al., 2018) of which more than 40 species in 25 genera have been domesticated for food, forage, and other uses (Smartt & Simmonds, 1995; Hammer & Khoshbakht, 2015; Table S2). To identify wild, perennial, herbaceous legume species, we extracted data from the International Legume Database and Information Service **(**ILDIS; www.ildis.org), a global cooperative database developed by 71 legume specialists (Bisby, 1993; Roskov et al., 2005; Roskov et al., 2017a). At the time of data extraction ILDIS included 19,939 species in 732 genera with 5,118 infra-specific taxon names. In addition, ILDIS includes information on life form, growth habit, conservation status, economic use, geographic distribution, illustrations, and maps (Roskov et al., 2005; Roskov et al., 2017a). These data were not accessible through ILDIS or Catalogue of Life; we acquired them directly from ILDIS database manager Y. Roskov as eight separate comma-separated value (.csv) files (Table S4).

ILDIS data query and filtering. We used MySQL (Widenius et al., 2002) to query each of the eight .csv files and extracted information describing growth habit (herb, shrub, or tree), lifespan (annual or perennial), taxon name, and ILDIS IDs. ILDIS IDs are unique record numbers that correspond to species, subspecies, and varieties, and serve as the only link between trait information and taxonomy in the ILDIS data. We wrote custom scripts in Visual FoxPro Version 9.0 (Microsoft, Redmond, Washington, USA) to match ILDIS IDs to their respective growth habit, lifespan, and taxonomic names (Appendix 1). From Visual FoxPro, we exported one single output file (.csv) for the ILDIS database assembly (Table S5; Figure S1; Figure S2). Not all ILDIS IDs in the database assembly file contained complete lifespan and growth habit trait data. When these data were missing, literature was consulted and gaps were filled manually (Figure

S1, Table S3). Further, ILDIS did not include information for biennials. ILDIS IDs that were missing both lifespan and growth habit information were removed from the database assembly file.

We used Microsoft Excel to filter the data. First, we discarded taxa listed as trees, trees/shrubs, and obligate shrubs. Second, we discarded annual herbs. Third, we removed intraspecific taxa (e.g., subspecies and varieties). Ultimately, we retained only ILDIS IDs for perennial, herbaceous species that grow as annuals in some environments, and perennial herbs that become shrubby in some environments.

Matching ILDIS species names in Tropicos database. To match species names extracted from ILDIS to species names in Tropicos (Figure S1), first we matched species names regardless of differences in authority and automatically selected the accepted name and authority when available. From Tropicos, we obtained a file that contained unique Tropicos IDs (species names in Tropicos) for each ILDIS species name. Trait data for species names were imported into Tropicos using their corresponding Tropicos ID, and subsequently linked automatically to taxonomic information, specimen information, references, photos, and distribution maps for that name in Tropicos. A number of species names present in ILDIS were missing in Tropicos. We verified ILDIS names in the International Plant Names Index (IPNI, 2012) and manually entered them in Tropicos. Species names present in ILDIS but absent from IPNI were not recorded in Tropicos and were removed from the database assembly file.

Establishment of PAPGI interface. Legume data extracted from ILDIS and imported into Tropicos were organized into a special project within Tropicos, the Perennial Agriculture Project Global Inventory (PAPGI; http://www.tropicos.org/Project/PAPGI). PAPGI has a user-friendly layout that includes a vertical navigation bar that links to PAPGI-specific information (project introduction, family descriptions, and a customized search builder). An important feature within PAPGI is the search builder, a custom query based on 63 traits organized into seven broad categories: 1) taxonomy, 2) growth descriptors, 3) ecology, 4) reproductive biology, 5) genetics, 6) economic use, and 7) toxicity (Table 2). Descriptors were developed with input from breeders at The Land Institute, who identified traits used when selecting perennial, herbaceous species for pre-breeding programs. PAPGI includes a drop-down menu for each descriptor. For example, under "reproductive biology" > "sexual reproduction," users can select "selfing" and run the search engine. Upon completion, this search will pull up all taxa in the database that are known to self-fertilize. It is possible to search for any combination of descriptors in the database; however it is important to note that data acquisition and entry is ongoing.

Ethnobotanical data integration within PAPGI. Ethnobotanical data were compiled from ILDIS, other databases, and literature (Table S6; National Research Council, 1979; Smartt, 1990). We assembled an ethnobotanical dataset for our list of wild, perennial, herbaceous Fabaceae species. We documented plant parts used for human consumption (flowers, leaves, pods, and seeds), food type description, as well as names and localities of indigenous tribes using them. Similarly, we recorded if a species was used for forage, fodder, silage, and any other economic applications, such as bioenergy, fiber, gums/resins, honey production, latex/rubber, medicinal/psychoactive properties, wax, and cultural or religious purposes (Table 2).

Toxicological data integration within PAPGI. Many plants are inedible to humans without some form of processing; consequently, information about plant toxicity and detoxification methods is important when considering wild taxa for pre-breeding. We entered toxic properties into PAPGI, such as the toxic part(s) of the plant and the nature of the toxicity report (i.e. observed in the lab, field, in animals or in humans; Table 2, Table S7).

The definition of "toxicity" is not straightforward and sometimes depends upon value judgment. For each species, we categorized reported toxicity as either toxic to humans, toxic to animals, or predicted as toxic. Edible plants for which there are occasional, idiosyncratic reports of negative reactions were generally not coded as toxic to humans, while well-defined and relatively common human illnesses associated with edible plants (e.g., favism) were flagged as "Toxicity - human." "Toxicity - animal" was used for reports of illness in livestock, including in controlled feeding studies or if an animal voluntarily consumed the plant. "Toxicity - lab animal" described species reported as toxic in studies in which small animals in confinement were overfed quantities of a plant or plant extract, since results of such studies are not always relevant to normal exposure. "Toxicity - predicted" was used to flag species without reports of illness, but that had been reported in survey studies to contain chemicals similar to other toxic species (in particular, Davis, 1982; Williams & Gómez-Sosa, 1986; Wink, Meisner, & Witte, 1995; Fletcher, Al Jassim, & Cawdell-Smith, 2015). Generally, we observed that species whose chemistry and bioactivity are understudied should similarly be suspected of toxicity when toxicity is common within the same genus. We have noted these observations on the PAPGI-specific webpages of several genera; however, comments are not exhaustive, and species with unknown toxicity should be investigated further (Table S7).

Results

PAPGI database construction - *Summary of extracted data from ILDIS***.** The ILDIS database reported 26,394 Fabaceae ILDIS IDs (species and infraspecific taxa) and 19,939 species names (Roskov et al., 2005). In this study we recovered slightly fewer taxon names from ILDIS (25,005 taxon names, 19,904 species); we believe the discrepancy was the result of edits made to the ILDIS database after its 2005 publication. Of these, 5,370 taxon names (3,974 species names) had incomplete or missing lifespan and growth habit trait data. We completed partially missing lifespan and growth traits for 59 taxon names and the remaining 5,311 taxon names (3,942 species) were not included in PAPGI. The significance of missing data for our database is minor as many missing species belong to woody genera (e.g. *Acacia*, *Caesalpinia*, *Mimosa* etc.) or genera with large number of species (e.g. *Astragalus*) where detailed taxonomic assessments are ongoing. Thus, of the 25,005 taxon names extracted, 19,694 taxon names (15,963 species names, 80.19% of the total in ILDIS) have complete trait data for lifespan and growth habits (Table 3). Of the 19,694 taxon names with trait data, 18,018 taxon names (14,645 species names) are perennial or perennial/annual, and 1,674 taxon names (1,317 species names) are annual (Table 3). One herbaceous taxon was determined to be biennial. 91.74% (14,645 of 15,963) of wild legume species examined for this study are perennial (Table 3 and Figure 2). Of these, 6,644 are primarily perennial and herbaceous. The remaining 2,904 tree taxa (2,439 species names), 1,619 shrub/tree taxa (1,300 species names), and 5,222 shrubby taxa (4,230 species names) were neither perennial nor herbaceous and were not included in PAPGI (Table 3).

PAPGI database construction - *Matching ILDIS species names in Tropicos database*

Of the 6,644 wild, primarily perennial herbaceous species names in ILDIS, we matched 6,427 to existing Tropicos records. 217 ILDIS species names were missing from Tropicos. Of these, 142 were retrieved in IPNI and recorded in Tropicos (see methods), the remaining names were not entered in Tropicos. In total, 6,569 perennial, herbaceous species (or herbaceous and shrubby, or annual/perennial herbaceous) derived from ILDIS were included in PAPGI. One caveat is that the ILDIS database represents approximately 95% of the living legume species in the world (Roskov pers. comm.), and species names are continually being added onto the database checklist as they are discovered (Roskov et al., 2017 a, b; Smýkal et al., 2018).

Agriculturally important trait data within PAPGI. PAPGI functions as an interface for the integration of agriculturally and ecologically important trait data (Table 2). This framework includes over 60 traits with drop-down selection options for each of the traits of interest. While trait information has been completed for some taxa (e.g., *Lupinus* spp.), most require additional data entry.

Ethnobotanical data for perennial, herbaceous Fabaceae. At present, PAPGI includes ethnobotanical data for 314 wild, perennial, herbaceous legume species, and 91 of these have economic uses other than food, including fiber and medicinal properties (Table S6). As human populations have become increasingly urbanized, human collection of edible plants from the wild has decreased drastically (Hunter, 2007). Therefore, some of the recorded uses should be regarded as historical.

PAPGI includes genera with both agriculturally important annual crops and perennial herbaceous species, including: *Arachis* (52 perennial species), *Cajanus* (11), *Cicer* (35), *Glycine* (26), *Lathyrus* (83), *Lupinus* (113), *Medicago* (40), *Phaseolus* (15) *Psophocarpus* (9), *Trifolium* (95), *Vavilovia formosa* (a wild relative of *Pisum sativum*), *Vicia* (79), and *Vigna* (50) (Table S2). Wild, herbaceous, perennial crop relatives include the perennial soybean species *Glycine tomentella* and *G. tabacina* consumed by aboriginal populations in Australia and in the Philippines. The perennial chickpea species *Cicer microphyllum* and *C. songharicum* are consumed by native peoples of middle Asia and the Himalayas. Also, six perennial *Phaseolus* species were consumed by Native Americans including *P. coccineus*, *P. lunatus*, *P. maculatus*, *P. polystachios*, as well as *P. filiformis*, and *P. ritensis* in the Sonoran desert (Table S6 and references within).

In addition to wild, perennial, herbaceous relatives of domesticated Fabaceae there are many other legume species that have been used by humans for various purposes, but that are not closely related to major crops (Table S6 and references within). For example, 16 perennial grasspea (*Lathyrus*) species are consumed by Native North American groups and African and Indian people. Seven perennial lupines (*Lupinus* spp.) are consumed by North and South American indigenous peoples. Eighteen perennial vetches (*Vicia* spp.) are consumed in North America, China, and Africa and are used as forage and fodder in multiple parts of the world. Sixteen perennial *Vigna* species are consumed primarily in South America and Africa. Other Fabaceae genera contain promising perennial species candidates that have been harvested for food and forage (Caradus & Williams, 1995), including *Apios* (4 perennial species), *Astragalus* (20) *Baptisia* (14), *Dalea* (87), *Desmanthus* (18), *Lespedeza* (27), *Lotus* (81), *Pediomelum* (7), and *Trigonella* (40).

Toxicological data for perennial, herbaceous Fabaceae species. 238 legume species were identified as toxic in PAPGI (Table S7 and references within). These include 15 species with known human toxicity, 118 species with animal toxicity, 26 species with animal toxicity in lab studies, and 80 species with predicted toxicity based on reported information (Table S7). Categories of toxins are also reported for most genera or for individual species, e.g. neurotoxic nitro compounds in *Astragalus* spp., pyrrolizidine alkaloids in *Crotalaria* spp., and *Lupinus* spp., anthraquinones in *Chamaecrista* spp. and *Senna* spp., cyanogenic glycosides in *Lotus* spp. etc. (Table S7). Seeds or fodder (forage bearing seeds) of 162 species were reported as toxic (Table S7). It should be noted that seeds of 17 species were coded as both “toxic” and “used as human food,” which may indicate loss of toxicity with appropriate processing or natural variation for toxicity. Six Fabaceae genera were also flagged as containing species with a high index of “suspicion for toxicity.” Although we present a summary of known toxicology information (Table S7), we recommend that for species with unknown toxicology information, users consult toxicity information recorded on the PAPGI genus page, because this information applies to all species within the genus. We predict that the number of legume species known to contain toxic compounds will increase dramatically as this field is populated. Therefore, additional research into toxic compounds for specific candidates is recommended before selection for pre-breeding.

Discussion

The Perennial Agriculture Project Global Inventory (PAPGI) bridges botanical diversity data and the plant breeding community, offering a taxonomically accurate and up-to-date inventory of wild, perennial, herbaceous legumes. This resource was designed to aid in the identification of perennial, herbaceous candidates for pre-breeding, domestication, and possible use in the ecological intensification of agriculture. Because PAPGI is embedded within Tropicos, it links directly to species names, collection records, locality data, and other botanical data. Further, PAPGI includes a searchable database of more than 60 agriculturally important traits, and incorporates taxon-specific information on ethnobotany and toxicology. Although many outstanding plant databases have been developed prior to the inception of this project, they catalogued either contemporary crops and their wild relatives, or wild plant diversity (Table S3). The novel contribution of PAPGI is its focus on wild, perennial, herbaceous species that generally have not entered the domestication process, that may or may not be related to existing crops, but that may hold promise for crop development.

Cataloging wild plant biodiversity to support agricultural innovation. Of the 15,963 legume species listed in ILDIS, 14,645 (91.74%) are perennial (Table 3 and Figure 2). This result is not surprising as many world ecosystems consist primarily of perennials (Zhang et al., 2011); however, domestication efforts have focused primarily on annual legumes, which in our study make up 8.25% of the family. Although many wild, perennial Fabaceae are woody (49.95%), there are 6,644 wild, perennial, herbaceous legume species (41.62% of the family). Previously, wild, perennial herbaceous legumes and their associated trait data (growth habit, economic uses and toxicological information) were not readily available nor easily searchable within ILDIS. PAPGI offers a tool for filtering and identifying wild, herbaceous, perennial species that might be good candidates for pre-breeding and domestication.

The PAPGI framework allows for queries that support both approaches to developing perennial, herbaceous crops: wide hybridization and *de novo* domestication (DeHaan et al., 2014). Breeders can use PAPGI to support wide hybridization by identifying perennial members of genera that contain annual crops. We queried 13 commercially produced herbaceous legume crops in PAPGI and found that these agriculturally important legume genera contain more perennial than annual species, and that many of their perennial species are edible or have forage uses (Tables S2 and S6). PAPGI can also be used to support *de novo* domestication. Although data entry is ongoing, PAPGI offers the opportunity to filter the 6,644 wild, perennial, herbaceous legumes through the selection of suites of traits. One way in which PAPGI might facilitate this initial selection process is to identify species that have been used by people (Table S6). Using data generated in PAPGI, we identified a "short-list" of 10 candidate genera with underutilized wild, perennial herbaceous/shrubby species used for food in temperate and tropical areas: *Apios* (4 perennial species), *Astragalus* (1,720), *Baptisia* (14), *Canavalia* (22), *Dalea* (86), *Macroptilium* (9), *Macrotyloma* (21), *Psophocarpus* (9), *Psoralea* (45), and *Tylosema* (4). These genera may be the focus of future analyses assessing in ground field traits and response to selection. Fabaceae results support previous predictions that wild, perennial, herbaceous species have the potential to expand agricultural diversity beyond current annual grain crops (Crews & Cattani, 2018).

PAPGI can be used in concert with ongoing projects as well. For example, breeders in Australia identified wild perennial, herbaceous legume crop candidates adapted to dry and hot climates, such as the genus *Cullen* (Bennett et al., 2011). *Cullen* includes 16 perennial herbaceous/shrubby species with deep taproots and good seed yield (Bell et al., 2011; Bell et al., 2012). Additional information on these taxa is available within PAPGI. Further, Schlautman et al. (2018) identified 43 temperate adapted perennial legume candidates with desirable pre-breeding traits, such as determinate growth, synchronous maturation, and non-shattering fruits. PAPGI expands upon this and includes perennial, herbaceous species of *Glycyrrhiza* (19 perennial, herbaceous species), *Onobrychis* (124), *Oxytropis* (472), *Senna* (21), and *Thermopsis* (25). Many perennial species of these genera have complete edibility and toxicity information in PAPGI (Tables S5 and S6 and references within).

Future directions to strengthen connections between botanical diversity and agriculture research. PAPGI represents an important conceptual and practical advance in the cataloging of wild plant biodiversity to support agricultural innovation. This database expands plant genetic resources for agriculture to include wild, perennial, herbaceous species (Van Tassel, DeHaan, & Cox, 2010; Meyer, DuVal, & Jensen, 2012). Using the PAPGI model, perennial herbaceous species from other families with economic crops (such as Brassicaceae, Polygonaceae, Solanaceae etc.) or desirable agronomic or ecological traits could be documented, thus enhancing the role of botanical sciences in describing diversity and delivering valuable perennial crop candidates.

A major challenge for PAPGI is the compilation and integration of detailed information on agriculturally important traits, such as breeding systems, genetics, and morphology. These data are often available from disparate sources in the literature and other databases. We developed a framework for data integration within PAPGI; however, efforts to place these valuable data into PAPGI consist primarily of manual entry. Important next steps include automated efforts to add data on agriculturally important traits (e.g. Endara, Cui, & Burleigh, 2018), and also to develop a system in which researchers around the world can contribute their data. Another long-term objective is to facilitate the acquisition of seeds or clones of species in the PAPGI database. Alternative cropping systems, such as perennial polycultures, require careful reconsideration of the conservation of Plant Genetic Resources for Agriculture (PGRFA) (Jackson & Ford-Lloyd, 1990; FAO, 2009; Heywood, 2011). Wild, perennial, herbaceous species of the Fabaceae and other families represent one possible expansion of the concept of PGRFA, with an eye towards wild plant biodiversity that might be useful in the ecological intensification of agriculture. PAPGI connects major botanical resources (e.g., Missouri Botanical Garden) with plant breeders (The Land Institute), thereby offering an important model for future efforts aimed at diversifying species used in agriculture.

In conclusion, the vast plant diversity in nature and in cultivation has been catalogued in various ways by different academic and research communities (Table S3). Although botanists, agronomists, ethnobotanists, ecologists, and farmers have complementary interests, the data being collected are not always available in a form that is easily accessible to all of the various research groups interested in plant diversity and agriculture. PAPGI attempts to connect taxonomic and agronomic databases to identify wild, previously undomesticated taxa for inclusion in breeding programs. A major challenge moving forward is the efficient extraction of data on plant form, function, and use from disparate, diverse sources including journal articles, books, and even herbarium specimens. Harvesting these valuable data, and integrating them in an efficient way into searchable, web-accessible databases like PAPGI, is a major hurdle that requires creative approaches and cutting-edge technologies.

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Author Contribution

A.J.M., W.A., J.M. and T.E.C. conceived the work. C.C., and A.J.M. developed of the manuscript with conceptual advice from W.A., T.E.C., L.R.D, D.V.T., B.S and J.M. Y.R.

generated the ILDIS data and provided taxonomy, nomenclature and data extraction guidance. R.M. designed the PAPGI database layout in Tropicos. N.C. queried and extracted ILDIS data, generated the output file, and wrote the scripting steps in the Appendix 1. A.T. and W.A. recorded ethnobotanical and toxicological data in PAPGI and wrote the corresponding methods and results in the manuscript. E.F., and S.A.H., reviewed literature, edited figures, tables, and the manuscript. R.M. implemented the PAPGI framework in Tropicos. J.Z. curated the taxonomy and nomenclature of new legume species in Tropicos. J.S. assisted with entering new species in Tropicos, and edited existing synonymy records. All authors read, edited, and reviewed the manuscript, discussed the presented ideas and approved the final manuscript.

Conflicts of Interest The authors declare no conflict of interest.

References

Bell, L.W., Bennett, R.G., Ryan, M.H., & Clarke, H. (2011). The potential of herbaceous native Australian legumes as grain crops: a review. *Renewable Agriculture and Food Systems*, 26 (1), 72-91. https://doi:10.1017/s1742170510000347.

Bell, L.W., Ryan, M.H., Bennett, R.G., Collins, M.T., & Clarke, H.J. (2012). Growth, yield and seed composition of native Australian legumes with potential as grain crops. *Journal Of The Science Of Food And Agriculture*, 92 (7), 1354-1361. https://doi:10.1002/jsfa.4706.

Bennett, R.G., Ryan, M.H., Colmer, T.D., & Real, D. (2011). Prioritisation of novel pasture species for use in water-limited agriculture: a case study of *Cullen* in the Western Australian wheatbelt. *Genetic Resources and Crop Evolution*, 58 (1), 83-100. https://doi:10.1007/s10722-010-9567-3.

Bingham, E., Haas,T., Irwin, J., Mackie, J., Musial, J., Armour, D., Scotti, C., Arcioni, S., Jimenez, C., & Mauriera, I. (2005). Alfalfa says hello to the genome of *Medicago arborea*.

Reports by Bingham and by Haas in: *Medicago Genetic Reports*, 5. Available at www.medicago-reports.org.

Bisby, F.A. (1993). Species Diversity Knowledge Systems: The ILDIS Prototype for legumes. *Annals of New York Academy of Sciences*, 700 (1), 159-164. https://nyaspubs.onlinelibrary.wiley.com/doi/abs/10.1111/j.1749-6632.1993.tb26316.x

Bommarco, R., Kleijn, D., & Potts, S.G. (2013). Review: Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, 28 (4), 230-238. https://doi: 10.1016/j.tree.2012.10.012.

Caradus, J.R., & Williams, W.M. (1995). Other temperate forage legumes (p.332-343). In: J. Smartt, & N.W. Simmonds (Eds.), *Evolution of Crop Plants*, 2nd Edition. Singapore: Longman Publishers.

Cassman, K.G. (1999). Ecological intensification of cereal production systems: Yield potential, soil quality, and precision agriculture. *Proceedings National Academy of Sciences*, 96 (11), 5952-5959. https://doi.org/10.1073/pnas.96.11.5952.

Cattani, D.J. (2014). Perennial polycultures: How do we assembly a truly sustainable agricultural system? In Perennial Crops for Food Security Proceedings of the FAO Expert Workshop. Rome, Italy.

Chen, Q.-F., Huang, X.-Y., Li, H.-Y., Yang, L.-J., & Cui, Y.-S. (2018). Recent Progress in Perennial Buckwheat Development. *Sustainability*, 10 (2), 536-553. https://doi:10.3390/su10020536.

Cox, T.S., Glover, J.G., Van Tassel, D.L., Cox, C.M., & DeHaan, L.R. (2006). Prospects for developing perennial grain crops. *Bioscience* 56, 649-659. https://doi.org/10.1641/0006-3568(2006)56[649:PFDPGC]2.0.CO;2.

Cox, S., Nabukalu, P., Paterson, A. Kong, W., & Nakasagga, S. (2018). *Development of Perennial Grain Sorghum. Sustainability*, 10 (1), 172-180. https://doi.org/10.3390/su10010172.

Crews, T.E., Blesh, J., Culman, S.W., Hayes, R.C., Jensen, E.S., Mack, M.C., Peoples, M.B., & Schipanski, M.E. (2016). Going where no grains have gone before: From early to mid-succession. *Agriculture Ecosystems & Environment*, 223, 223-238. https://doi.org/10.1016/j.agee.2016.03.012.

Crews, T.E. & Cattani, D.J. (2018). Strategies, Advances, and Challenges in Breeding Perennial Grain Crops. *Sustainability*, 10 (7), 2192-2199. https://doi:10.3390/su10072192.

Davis, A.M. (1982). The occurrence of anagyrine in a collection of western American lupines. *Journal of Range Management*, 35, 81–84.

DeHaan, L.R., Van Tassel, D.L. & Cox, T.S. (2005). Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems*, 20 (1), 5-14. https://doi: 10.1079/RAF200496.

DeHaan, L.R., & Van Tassel, D.L. (2014). Useful insights from evolutionary biology for developing perennial grain crops. *American Journal of Botany*, 101 (10), 1801-1819. https://doi: 10.3732/ajb.1400084.

DeHaan, L.R., Van Tassel, D.L., Anderson, J.A., Asselin, S.R., Barnes, R., Baute, G.J., Cattani, D.J., Culman, S.W., Dorn, K.M., Hulke, B.S., Kantar, M., Larson, S., Marks, M.D., Miller, A.J., Poland, J., Ravetta, D.A., Rude, E., Ryan, M.R., Wyse, D., & Zhang, X.F. (2016). A Pipeline Strategy for Grain Crop Domestication. *Crop Science*, 56 (3), 917-930. https://doi: 10.2135/cropsci2015.06.0356.

DeHaan, L., Christians, M., Crain, J., & Poland, J. (2018). Development and evolution of an intermediate wheatgrass domestication program. *Sustainability*, 10 (5), 1499- 1518. https://doi.org/10.3390/su10051499.

Doré, T., Makowski, D., Malézieux, E., Munier-Jolain, N., Tchamitchian, M., & Tittonell, P. (2011). Facing up to the paradigm of ecological intensification in agronomy: Revisiting methods, concepts and knowledge. *European Journal of Agronomy*, 34, 197–210. https://doi:10.1016/j.eja.2011.02.006.

Endara, L., Cui, H., & Burleigh, J.G. (2018). Extraction of phenotypic traits from taxonomic descriptions for the tree of life using natural language processing. *Applications in Plant Sciences*, 6(3), e1035. https://doi:10.1002/aps3.1035.

Fletcher, M.T., Al Jassim, R.A.M., & Cawdell-Smith, A.J. (2015). The occurrence and toxicity of indospicine to grazing animals. *Agriculture*, 5 (3), 427–440. https://doi.org/10.3390/agriculture5030427.

Food and Agriculture Organization of the United Nations (FAO) (2009). A Global Treaty for Food Security and Sustainable Agriculture, International Treaty on plant genetic resources for food and agriculture. FAO, Rome: Electronic Publishing Policy and Support Branch Communication Division.

Glover, J.D., Reganold, J.P., Bell, L.W., Borevitz, J., Brummer, E.C., Buckler, E.S., Cox, C.M., Cox, T.S., Crews, T.E., Culman, S.W., DeHaan, L.R., Erickson, D., Gill, B.S., Holland, J., Hu F., Hulke, B.S., Ibrahim, A.M.H., Jackson, W., Jones, S.S., Murray, S.C., Paterson, A.H., Ploschuk, E., Sacks, E.J., Snapp, S., Tao, D., Van Tassel, D.L., Wade, L.J., Wyse, D.L., & Xu Y. (2010). Increased Food and Ecosystem Security via Perennial Grains, *Science* 328, 1638 – 1639.

Hammer, K., & Khoshbakht, K. (2015). A domestication assessment of the big five plant families. *Genetic Resources and Crop Evolution*, 62 (5), 665-689. https://doi.org/10.1007/s10722-014-0186-2.

Hayes, R.C., Wang, S., Newell, M.T., Turner, K., Larsen, J., Gazza, L., Anderson, J.A., Bell, L.W., Cattani, D.J., Frels, K., Galassi, E., Morgounov, A.I., Revell, C.K., Thapa, D.B., Sacks, E.J., Sameri, M., Wade, L.J., Westerbergh, A., Shamanin, V., Amanov, A., & Li, G.D. (2018). The performance of early-generation perennial winter cereals at 21 sites across four continents. *Sustainability*, 10 (4), 1124-1152. https://doi.org/10.3390/su10041124.

Heywood, V.H. (2011). Introduction of Crop Wild Relatives (CWR) (p. 1-28). In: D. Hunter, & V.H. Heywood (Eds.), *Crop Wild Relatives: A Manual of in situ Conservation*. London: Earthscan and Bioversity International. Available at: https://www.bioversityinternational.org/fileadmin/user_upload/online_library/publications/pdfs/Crop_wild_relatives/1.Introductory_background.pdf.

Huang, G., Qin, S., Zhang, S., Cai, X.,Wu, S., Dao, J., Zhang, J., Huang, L., Harnpichitvitaya, D., Wade, L., & Hu, F. (2018). Performance, economics and potential impact of perennial rice PR23 relative to annual rice cultivars at multiple locations in Yunnan Province of China. *Sustainability*, 10 (4), 1086-1104. https://doi.org/10.3390/su10041086.

Hunter, P. (2007). The human impact on biological diversity. How species adapt to urban challenges sheds light on evolution and provides clues about conservation. Analysis Science and Society. *European Molecular Biology Organization (EMBO) Reports*, 8 (4), 316-318. https://doi: 10.1038/sj.embor.7400951.

The International Plant Names Index (IPNI) (2012). Published on the Internet http://www.ipni.org [accessed March and May 2017]

Irwin, J.A.G., Sewell, J.C.,Woodfield, D.R., & Bingham, E.T. (2016). Restructuring lucerne (*Medicago sativa*) through introgression of the *Medicago arborea* genome. *Agricultural Science,* 28 (1), 40-46.

Jackson, M.T., & Ford-Lloyd, B.V. (1990). Plant genetic resources - a perspective (p.1-17). In: M.T. Jackson, B.V. Ford-Lloyd, & M.L. Parry (Eds.), *Climatic Change and Plant Genetic Resources*. London: Belhaven Press.

Kantar, M.B., Tyl, C. E., Dorn, K.M., Zhang, X., Jungers, J.M., Kaser, J.M., Schendel, R.R., Eckberg, J.O., Runck, B.C., Bunzel, M., Jordan, N.R., Stupar, R.M., Marks, M.D., Anderson, J.A., Johnson, G.A., Sheaffer, C.C., Schoenfuss, T.C., Ismail, B., Heimpel, G.E., & Wyse, D.L. (2016). *Annual Reviews of Plant Biology*, 67, 703-29. https://doi:10.1146/annurev-arplant-043015-112311.

Lewis, G., Schrire, B., & Lock, M. (2005). *Legumes of the World*. Richmond: Kew Publishing.

Mann, C. (1997). Reseeding the Green Revolution. *Science*, 277 (5329), 1038-1043.

Meyer, R.S., DuVal, A.E., & Jensen, H.R. (2012). Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist Trust*, 196 (1), 29-48. https://doi: 10.1111/j.1469-8137.2012.04253.x.

Millennium Ecosystem Assessment (2005). Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

National Research Council (1979). *Tropical legumes: Resources for the future*. Washington: National Academy of Sciences.

Pimentel, D., Cerasale, D., Stanley, R.C., Perlman, R., Newman, E.M., Brent, L.C., Mullan, A., & Chang, D.T.-I. (2012). Annual vs. perennial grain production. *Agriculture, Ecosystems and Environment*, 161, 1-9. http://dx.doi.org/10.1016/j.agee.2012.05.025.

Pretty, J., Toulmin, C., & Williams, S. (2011). Sustainable Intensification in African Agriculture. *International Journal of Agricultural Sustainability*, 9 (1), 5-24. https://doi.org/10.3763/ijas.2010.0583.

Roskov, Y., Bisby, F., Zarucchi, J., Schrire, B., & White, R. (Eds.) (2005). ILDIS World Database of Legumes: draft checklist, version 10 (November 2005). Mini CD-ROM; ILDIS: Reading, UK. ISBN 070491-2481.

Roskov, Y., Zarucchi, J., Novoselova, M., & Bisby, F.(†) (Eds) (2017a). ILDIS World Database of Legumes (version 12, May 2014). In: Species 2000 & ITIS Catalogue of Life, 2017 Annual Checklist (Roskov, Y., Abucay, L., Orrell, T., Nicolson, D., Bailly, N., Kirk, P.M., Bourgoin, T., DeWalt, R.E., Decock, W., De Wever, A., Nieukerken, E. van, Zarucchi, J., Penev, L., eds.). Digital resource at www.catalogueoflife.org/annual-checklist/2017. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-884X.

Roskov, Y., Zarucchi, J., Novoselova, M., & Bisby, F.(†) (Eds) (2017b). ILDIS World Database of Legumes (version 12, May 2014). In: Y. Roskov et al. (Eds.) (2017). Species 2000 & ITIS Catalogue of Life, 29th November 2017. Digital resource at www.catalogueoflife.org/col. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-8858.

Ryan, M.R., Crews, T.E., Culman, S.W., Dehaan, L.R., Hayes, R.C., Jungers, J.M., & Bakker, M.G. (2018). Managing for Multifunctionality in Perennial Grain Crops. *Bioscience*, 68 (4), 294 - 304. https://doi.org/10.1093/biosci/biy014.

Schlautman, B., Barriball, S., Ciotir, C, Herron, S., & Miller, A.J. (2018) Perennial Grain Legume Domestication Phase I: Criteria for Candidate Species Selection. *Sustainability*, 10 (3), 730-753. https://doi:10.3390/su10030730.

Smartt, J. (1990). *Grain legumes: evolution and genetic resources*. Cambridge: Cambridge University Press.

Smartt, J., & Simmonds, N.W. (Eds.) (1995). *Evolution of Crop Plants, 2nd Edition*. Singapore: Longman Publishers.

Smýkal, P., Nelson, M.N., Berger, J.D., & von Wettberg, E.J.B. (2018). The impact of genetic changes during crop domestication. *Agronomy*, 8 (26), 119-141. https://doi:10.3390/agronomy8030026.

Tang, Q., Rong, T., Song, Y., Yang, J., Pan, G., Li, W., Huang, Y., & Cao, M. (2005). Introgression of Perennial Teosinte Genome into Maize and Identification of Genomic In Situ Hybridization and Microsatellite Markers. *Crop Science*, 45, 717-721.

Tittonell, P. (2014). Ecological intensification of agriculture — sustainable by nature. *Current Opinion in Environmental Sustainability*, 8, 53-61. https://doi.org/10.1016/j.cosust.2014.08.006.

Van Tassel, D., DeHaan, L.R., & Cox, T.S. (2010). Missing domesticated plant forms: can artificial selection fill the gap? *Evolutionary Applications* 3 (5-6), 434-452. https://doi:10.1111/j.1752-4571.2010.00132.x.

Van Tassel, D.L., & DeHaan, L.R. (2013). Wild Plants to the Rescue. A reprint from the American Scientist, 1, 218-227. Available at: https://www.americanscientist.org/article/wild-plants-to-the-rescue.

Van Tassel, D.L., Albrecht, K.A., Bever, J.D., Boe, A.A., Brandvain, Y., Crews, T.E., Gansberger, M., Gerstberger, P., González-Paleo, L., Hulke, B. S., Kane, N. C., Johnson, P. J., Pestsova, E.G., Picasso Risso, V.D., Prasifka, J.R., Ravetta, D.A., Schlautman, B., Sheafer, C.C., Smith, K.P., Speranza, P. R., Turner, K. M., Vilela, A.E., von Gehren, P., & Wever, C. (2017). Accelerating *Silphium* Domestication: An Opportunity to Develop New Crop Ideotypes and Breeding Strategies Informed by Multiple Disciplines. *Crop Science* 57, 1274-1284. https://doi: 10.2135/cropsci2016.10.0834.

Vilela, A., González-Paleo, L., Turner, K., Peterson, K., Ravetta, D., Crews, T., & Van Tassel, D.L. (2018). Progress and Bottlenecks in the Early Domestication of the Perennial Oilseed *Silphium integrifolium*, a Sunflower Substitute. *Sustainability*, 10 (3), 638-661. https://doi:10.3390/su10030638.

Widenius, M., & Axmark, D. (2002). Mysql Reference Manual (1st ed.). Paul DuBois (Ed.). O'Reilly & Associates, Inc., Sebastopol, CA, USA. ISBN:0596002653

Williams, M.C., & Gómez-Sosa, E. (1986). Toxic nitro compounds in species of *Astragalus* (Fabaceae) in Argentina. *Journal of Range Management*, 39 (4), 341-344. https://doi: 10.2307/3899776.

Wink, M., Meisner, C., & Witte, L. (1995) Patterns of quinolizidine alkaloids in 56 species of the genus *Lupinus*. *Phytochemistry*, 38, 139-153. https://doi.org/10.1016/0031-9422(95)91890-D.

Zhang, Y., Li, Y., Jiang, L., Tian, C., Li, J., & Xiao, Z. (2011). Potential of Perennial Crop on Environmental Sustainability of Agriculture. *Procedia Environmental Sciences*, 10 (Part B), 1141-1147. https://doi.org/10.1016/j.proenv.2011.09.182.

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Supporting Information

Table S1. Some perennial, herbaceous species cultivated for fruits and seeds, below-ground structures, or vegetative components; many of these are planted as annual crops.

Table S2. Legume genera with domesticated species cultivated mainly for food, forage, and other uses. Crop species may be herbaceous annual, herbaceous perennial, or woody perennial. Superscripts for scientific names of crop species denote the following categories *= perennial herbaceous species cultivated as annual, +=perennial herbaceous species, grown for multiple years, and #=woody perennial; annual species have no marking symbol. Total number of species is completed from ILDIS (Roskov et al., 2005), and Lewis, Schrire, & Lock, 2005. The annual/perennial number of species is completed from ILDIS, Kole (Ed.), 2011, and PAPGI (Ciotir et al., 2016). All references are abbreviated and listed in the footnote.

Table S3. Existing databases that focus on crops and their wild relatives, wild plant diversity, taxonomy, general plant traits, and digitized specimens. Major biodiversity information portals to which Tropicos is connected are indicated by *.

Methods: Appendix S1. Document with detailed description of eight ILDIS legume data files, and the code of data extraction.

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Table S5. Raw ILDIS data extracted using MySQL, Visual FoxPro, and Excel software. Headings include unique ID number, lifespan (annual, perennial), growth habit (herb, shrub, and tree), genus name, genus name author, species name, species name author, subspecies/variety name, and subspecies/variety name author.

Table S6. Ethnobotanical data for 314 perennial herbaceous/shrubby species of the Fabaceae family extracted from PAPGI.

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Figure S1. Conceptual workflow chart for ILDIS database extraction and PAPGI construction.

Figure S2. Workflow executed for ILDIS database extraction. The raw data has been imported into Microsoft Excel and MySQL, executing MySQL queries and Visual FoxPro scripts to match each lifespan and habit trait to its specific ID and taxon name.

Table 1. Some perennial grain crops currently under development.

Crop common name	**Scientific name**	**Family**	**Reference**
Perennial alfalfa hybrid	*Medicago sativa* x *M. arborea* (L.)	Fabaceae	Bingham et al., 2005; Irwin et al., 2016
Perennial buckwheat	*Fagopyrum cymosum* (Trevir.) Meisn.	Polygonaceae	Chen et al., 2018
Intermediate wheatgrass or Kernza®	*Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey	Poaceae	DeHaan et al., 2018
Perennial maize	(*Zea diploperennis* (Iltis, Doebley & R. Guzman))	Poaceae	Kantar et al., 2016
Perennial maize hybrid	*Zea mays* (L.) x *Zea diploperennis*	Poaceae	Tang et al., 2005
Perennial rice	*Oryza sativa* × *Oryza longistaminata*	Poaceae	Huang et al., 2018
Rosinweed	*Silphium integrifolium* (Michx.)	Asteraceae	Van Tassel et al., 2017; Vilela et al., 2018
Perennial sorghum	*Sorghum bicolor* (L.) Moench x *S. halepense* (L.) Pers)	Poaceae	Cox et al., 2018
Perennial wheat	*Triticum aestivum* L.× *Thinopyrum Intermedium* (Host) Barkworth and D.R. Dewey	Poaceae	Hayes et al., 2018

Table 2. Perennial Agriculture Project Global Inventory (PAPGI) Search builder housed within the botanical database TROPICOS. For each general description category, specific trait types and descriptors were identified. In PAPGI, users can search legumes by trait.

General description category	**Trait type**	**Specific descriptor(s) with taxonomic and breeding ability**
Taxonomy and classification	Family, Genus, Species	Text box
General growth descriptors	Lifespan	Annual, Biennial, Perennial, Unknown
	Life form	Herbaceous, Shrub, Subshrub, Tree, Vine
	Plant-human relationship	Cultivated, Noxious weed, Wild, Unknown
	Photoperiodism	Day length neutral, Day length sensitive, Unknown
	Plant habit	Climbing, Cushion, Erect, Graminoid, Prostrate, Scrambling, Sprawling, Turf, Tussock, Twining, Unknown
	Stem type	Solitary, Multiple
	Vernalisation	No, Yes, Unknown
Ecology	Biogeographic realm	Australasian, Antarctic, Afrotropical, Indo-Malayan, Neartic, Neotropical, Oceanic, Paleartic
	Climatic zone	Boreal, Mediterranean, Montane, Subtropical, Temperate, Tropical, Tundra
	Conservation status	Critically Endangered, Data Deficient, Endangered, Extinct, Extinct in the Wild, Least Concern, Near Threatened, Not Evaluated, Vulnerable
	Elevation	Below sea level, 0 > 4500 m, Unknown
	Mycorrhizal associations	Yes, No, Unknown
	Nitrogen fixation	Yes, No, Unknown
	Seed dispersal in nature	Bird, Insect, Mammal, Water
	Tolerance(s)	Drought, Fire, Wind, Frost, Nutrient poor soil, Pathogens, Pests, Salinity, Shade
	Vegetation type	Anthropogenic, Coastlines/beaches/sand, Coniferous forest, Desert, Disturbed grassland, Dry broadleaf forest, Grassland, Humid broadleaf forest, Mangrove forest, Meadow, Mixed forests, Mountainsides/dry slopes, Roadsides, Savanna, Shrubland, Steppe, Xeric shrublands Swamp/marsh, Tundra, Volcanic soil vegetation
Reproductive biology	Asexual reproduction (apomixis)	Agamospermy, Apogamy, Apospory, Parthenogenesis, Unknown
	Sexual reproduction	Outcrossing, Selfing (cleistogamous), Unknown
	Vegetative reproduction	Bulbs, Cuttings, Rhizomes, Stolons, Tubers, Unknown

	Floral and plant sex	Androdioecious, Androgynomonoecious, Andromonoecious, Dioecious, Gynodioecious, Gynomonoecious, Hermaphroditic/bisexual flowers, Polygamodioecious, Polygamomonoecious, Monoecious, Unknown
	Unisexual floral distribution	Axillary, Caulinary, Terminal, Unknown
	Inflorescence type	Capitulum, Catkin, Corymb, Cyme, Panicle, Pseudoraceme, Raceme, Solitary flowers, Spadix, Spike, Umbel, Unknown
	Inflorescence position	Axillary, Terminal, Unknown
	Pollination	Birds, Insects, Mammals, Wind, Unknown
	Fruit dehiscence	Dehiscent, Indehiscent, Partially dehiscent, Unknown
	Fruit persistence	Persistent, Shattering, Unknown
	Details: Fruit shape and size	Open response
	Seeds per fruit	1, 2-5, 6-10, >10
	Seed color	Open response
	Seed size	Open response
	Seed description	Open response
	Germination requirements	Moisture treatment, Long-term storage, Nicking, None, Scarification, Short-term storage
	Seed dormancy breaking	Chemical scarification, Hormone treatment, Long-term storage, Mechanical scarification, Other, Short-term storage, Stratification, Temperature cycling
	Details: Seed dormancy breaking	Open response
	Seed storage behavior and longevity	Orthodox, Recalcitrant, Indefinite, Short, Unknown
	Seedling emergence	Delicate/slow, Vigorous/rapid
	Details: Seed viability	Open response
Genetics	Analyses of genetic variation	AFLP, Chloroplast sequence data, Microsatellites, Mitochondrial sequence data, Nuclear sequence data, Plastid sequence data, SNP analysis via reduced representation sequencing (GBS, Rad-seq, other)
	Genome sequence	Yes, No
	Assessment of genetic basis of phenotypic variation	GWAS study, QTL analysis, Transformation
	Ploidy	2x, 3x, 4x, 6x, 7x, 8x,10x, Other, Unknown
	Details: Genetics	Open response
Economic use	Domestic animal edible	Fodder, Forage, Silage

	Human edible	Below-ground structures, Flowers, Fruits, Leaves, Seeds, Stems
	Other uses	Bioenergy, Cultural or religious significance, Fiber, Gums/resins, Honey production, Latex/rubber, Waxes, Medicinal/psychoactive, Other properties
Toxicity	Toxicity	Animal, Human, Predicted
	Toxic parts	Flowers, Forage with seed, Leaves, Pods, Roots, Seeds, Silage, Stems
	Details: Toxicity	Open response

Table 4. Summary of taxon names and species names extracted from the International Legume Database and Information Service (ILDIS) organized according to lifespan and habit combination traits. Each row is exclusive of the others, such that only taxa with that exact combination of traits were counted for the row (e.g., only perennial and herbaceous and shrubby taxa in the first row). That is, the taxa in the first row are perennials which may be found in both a herbaceous and shrubby form. Bold font denotes categories that were retained from ILDIS, matched in Tropicos, and imported in PAPGI (e.g. perennial and herbaceous, or perennial/annual herbaceous, or perennial herbaceous/shrubby).

Lifespan	**Habit**	**#Taxa**	**#Species**
Perennial	**Herb/Shrub**	**1,834**	**1,482**
Perennial	**Herb**	**5,933**	**4,817**
Perennial	Tree	2,904	2,439
Perennial	Shrub/Tree	1,619	1,300
Perennial	Shrub	5,222	4,230
Perennial	Herb/Shrub/Tree	25	23
Perennial	Herb/Tree	3	3
Annual, Perennial	**Herb/Shrub**	**159**	**117**
Annual, Perennial	**Herb**	**311**	**228**
Annual, Perennial	Tree	1	1
Annual, Perennial	Shrub/Tree	3	2
Annual, Perennial	Shrub	4	3
Annual Biennial	Herb/Shrub/Tree	2	1
Annual	Herb/Shrub	5	4
Annual	Herb/Shrub/Tree	1	1
Annual	Shrub	1	1
Annual	Herb	1,667	1,311
Taxon names with complete traits		19,694	15,963
Taxon names with missing traits		5,311	3,941
Total number of taxon names		25,005	19,904

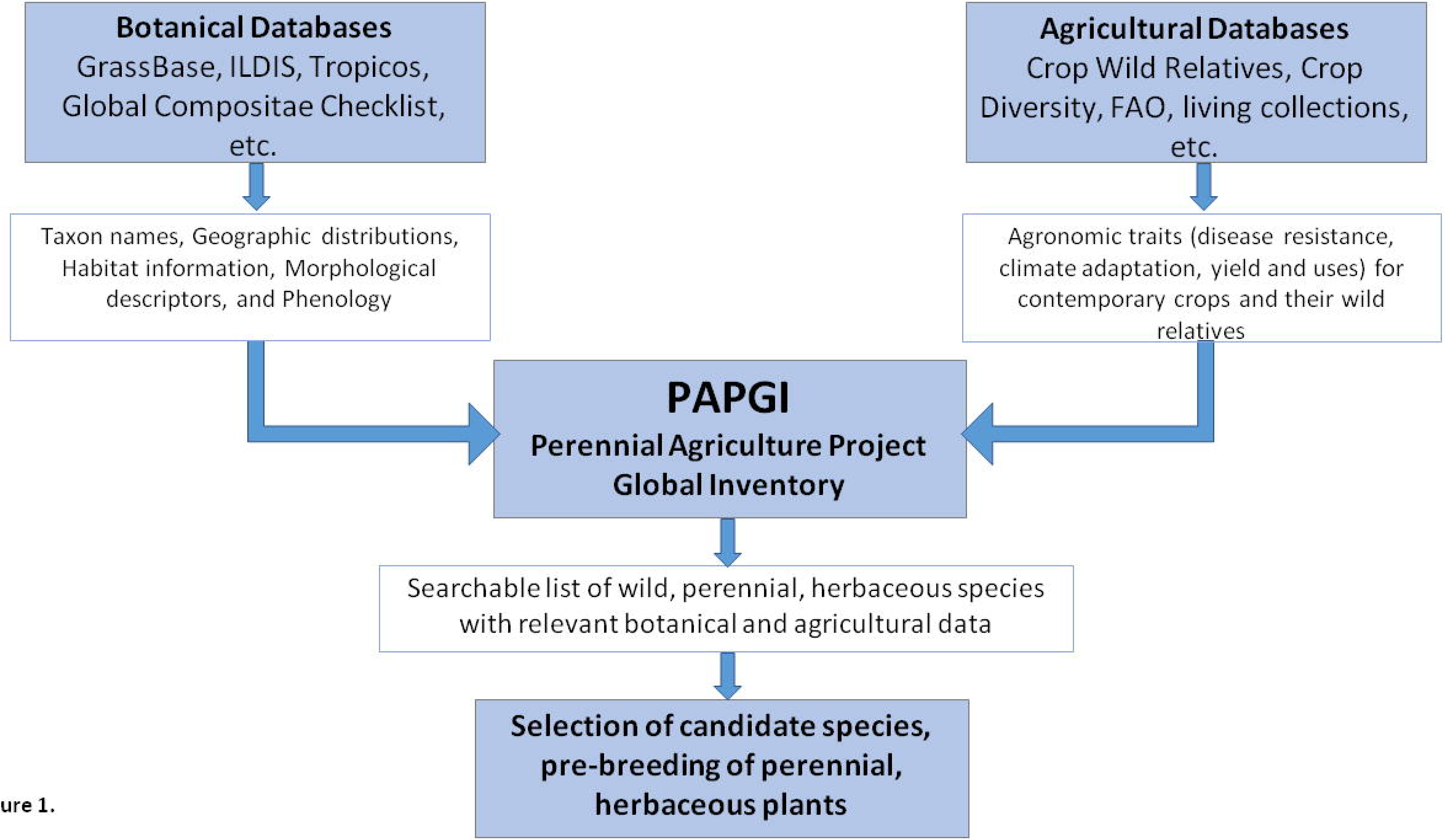
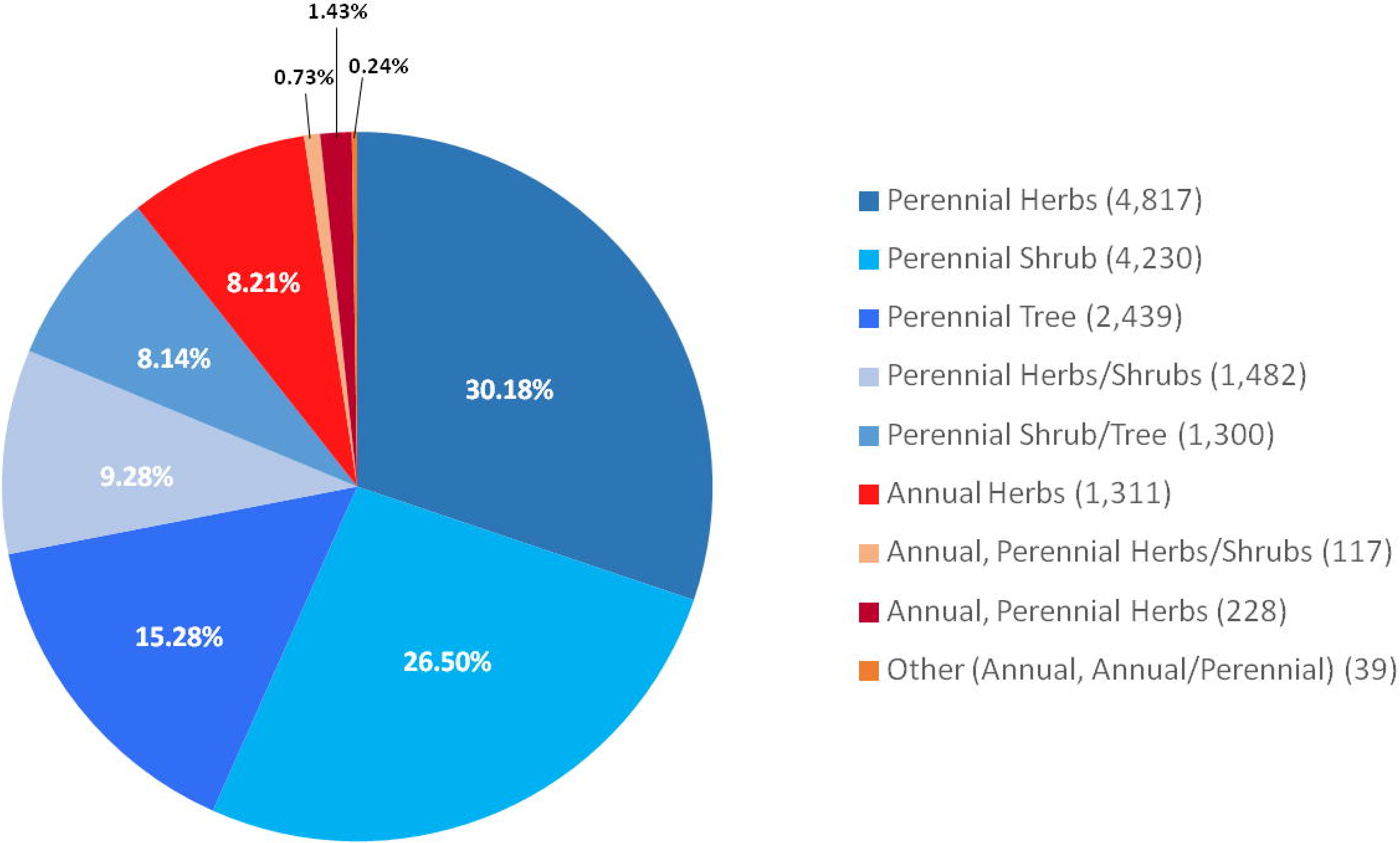

Botanical Databases
GrassBase, ILDIS, Tropicos, Global Compositae Checklist, etc.
Agricultural Databases
Crop Wild Relatives, Crop Diversity, FAO, living collections, etc.
Taxon names, Geographic distributions, Habitat information, Morphological descriptors, and Phenology
Agronomic traits (disease resistance, climate adaptation, yield and uses) for contemporary crops and their wild relatives
PAPGI
Perennial Agriculture Project Global Inventory
Searchable list of wild, perennial, herbaceous species with relevant botanical and agricultural data
Selection of candidate species, pre-breeding of perennial, herbaceous plants

Figure 1.



1.43%
0.73%
0.24%
8.21%
8.14%
30.18%
9.28%
15.28%
26.50%
Perennial Herbs (4,817)
Perennial Shrub (4,230)
Perennial Tree (2,439)
Perennial Herbs/Shrubs (1,482)
Perennial Shrub/Tree (1,300)
Annual Herbs (1,311)
Annual, Perennial Herbs/Shrubs (117)
Annual, Perennial Herbs (228)
Other (Annual, Annual/Perennial) (39)

Figure 2.