1 The International Weed Genomics Consortium: Community 2 Resources for Weed Genomics Research

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54	Abstract
55	The International Weed Genomics Consortium is a collaborative group of researchers focused on
56	developing genomic resources for the study of weedy plants. Weeds are attractive systems for
57	basic and applied research due to their impacts on agricultural systems and capacity to swiftly
58	adapt in response to anthropogenic selection pressures. Our goal is to use genomic information to
59	develop sustainable and effective weed control methods and to provide insights about biotic and
60	abiotic stress tolerance to assist crop breeding. Here, we outline resources under development by
61	the consortium and highlight areas of research that will be impacted by these enabling resources.
62	
63	Introduction
64	Each year globally, agricultural producers and landscape managers spend billions of US
65	dollars [1, 2] and countless hours attempting to control weedy plants and reduce their adverse
66	effects. These management methods range from low-tech (e.g., pulling plants from the soil by
67	hand) to extremely high-tech (e.g., computer vision-controlled spraying of herbicides).

68 Regardless of technology level, effective control methods serve as strong selection pressures on 69 weedy plants, and often result in rapid evolution of weed populations resistant to such methods 70 [3-7]. Thus, humans and weeds have been locked in an arms race, where humans develop new or 71 improved control methods and weeds adapt and evolve to circumvent such methods. 72 Applying genomics to weed science will enable the development of more sustainable and 73 effective control methods and offer a unique opportunity to study rapid adaptation and 74 evolutionary rescue of diverse weedy species in the face of widespread and powerful selective 75 pressures. Furthermore, lessons learned from these studies may also help to improve crop 76 breeding efforts in the face of our ever-changing climate. While other research fields have used 77 genetics and genomics to uncover the basis of many biological traits [8-11] and to understand 78 how ecological factors affect evolution [12, 13], the field of weed science has lagged behind in 79 the development of genomic tools essential for such studies [14]. As research in human and crop 80 genetics pushes into the era of pangenomics, (i.e., multiple chromosome scale genome 81 assemblies for a single species [15, 16]) publicly available genomic information is still lacking or 82 severely limited for the majority of weed species. In fact, a recent review of current weed 83 genomes identified just 26 weed species with sequenced genomes [17] – many assembled to a 84 sub-chromosome level.

The International Weed Genomics Consortium (IWGC) is an open collaboration between academic, government, and industry researchers focused on producing genomic tools for weedy species from around the world. Through this collaboration, our initial aim is to provide chromosome-level reference genome assemblies for at least 50 important weedy species from across the globe. Each genome will include annotation of gene models and repetitive elements and will be free to the public with no intellectual property restrictions. Species were chosen

based on member input, economic impact, and global prevalence (Figure 1). Additionally, future
funding of the IWGC will focus on supplementing these reference genomes with tools that
increase their utility.

94 The IWGC held its first conference in Kansas City, Missouri, USA in September of 2021. At 95 this meeting, guest speakers highlighted successful examples of using genomics to address 96 questions in weed science [5, 18-20]. Training workshops taught commonly used bioinformatic 97 pipelines, and oral and poster sessions showcased current research activities in weed genomics. 98 At the conclusion of this meeting, attendees participated in a forward-looking discussion about 99 the future of genomics in weed science and how the IWGC can help facilitate its successful 100 implementation. In this paper, we summarize the goals of the IWGC and how we plan to provide 101 support around the resources being developed to ensure they are widely accessible and utilized 102 by the research community. We go on to highlight areas of research where these tools can be 103 applied with hopes of attracting researchers from other fields to integrate weed science with the 104 many other research areas where genomic tools are being successfully utilized, enabling new 105 research towards adaptation, evolution, herbicide resistance, and genome biology.

106

107 Development of Weed Genomics Resources by the IWGC

108 *Reference genomes and data analysis tools*

109 The first objective of the IWGC is to provide high quality genomic resources for

agriculturally important weeds. The IWGC therefore created two main resources for information

- about, access to, or analysis of weed genomic data (Figure 1). The IWGC website [21]
- 112 communicates the status and results of genome sequencing projects, information on training and
- 113 funding opportunities, upcoming events, and news in weed genomics. It also contains details of

114 all sequenced species including genome size, ploidy, chromosome number, herbicide resistance 115 status, and reference genome assembly statistics. The IWGC either compiles existing data on 116 genome size, ploidy, and chromosome number, or obtains the data using flow cytometry and 117 cytogenetics (Figure 1; Additional File 1). Through this website, users can create an account to 118 access our second main resource, an online genome database called WeedPedia. WeedPedia 119 hosts IWGC-generated and other relevant publicly accessible genomic data as well as a suite of 120 bioinformatic tools. Unlike what is available for other fields, weed science did not have a 121 centralized hub for genomics information, data, and analysis prior to the IWGC. Our intention in 122 creating WeedPedia is to encourage collaboration and equity of access to information across the 123 research community. 124 WeedPedia is a cloud-based omics database management platform built from the software 125 'CropPedia', and licensed from KeyGene (Wageningen, The Netherlands). The interface allows 126 users to access, visualize, and download genome assemblies along with structural and functional 127 annotation. The platform includes a genome browser, comparative map viewer, pangenome 128 tools, RNA-sequencing data visualization tools, genetic mapping and marker analysis tools, and 129 alignment capabilities that allow searches by keyword or sequence. Additionally, genes encoding 130 known target sites of herbicides have been specially annotated, allowing users to quickly identify 131 and compare these genes of interest. The platform is flexible, making it compatible with future 132 integration of other data types such as epigenetic or proteomic information. As an online 133 platform with a graphical user interface, WeedPedia provides user-friendly, intuitive tools that 134 encourage users to integrate genomics into their research. We aspire for WeedPedia to mimic the

135 success of other public genomic databases such as NCBI, CoGe, Phytozome, InsectBase, and

136 Mycocosm to name a few. Additionally, all genome assemblies and annotations produced

137 through the IWGC will be uploaded to NCBI GenBank upon release (Table 1). WeedPedia 138 currently hosts 36 reference genomes with additional genomes in the pipeline to reach a currently 139 planned total of 50 reference genomes (Table 1). These genomes include both *de novo* reference 140 genomes generated or in progress by the IWGC (31 species; Table 1), and publicly available 141 genome assemblies of 19 weedy or related species (Table 2). As of June 2023, WeedPedia has 142 over 250 registered users representing 27 countries spread across 6 continents. 143 The IWGC reference genomes are generated in partnership with the Corteva Agriscience 144 Genome Center of Excellence (Johnston, Iowa) using a combination of single molecule long read 145 sequencing, optical genome maps, and chromosome conformation mapping. This strategy has 146 yielded highly contiguous, phased, chromosome-level assemblies for 20 weed species, with 147 additional assemblies currently in progress (Table 1). The IWGC assemblies have been 148 completed as single or haplotype-resolved double-haplotype pseudomolecules in inbreeding and 149 outbreeding species, respectively, with multiple genomes being near gapless. For example, the de 150 novo assemblies of the allohexaploids Conyza sumatrensis and Chenopodium album, have all 151 chromosomes captured in single scaffolds and most chromosomes being gapless from telomere 152 to telomere. Complementary full-length isoform (IsoSeq) sequencing of RNA collected from 153 diverse tissue types and developmental stages assists in the development of gene models during 154 annotation. Finally, the use of PacBio Revio has enabled the re-sequencing of 80 relevant 155 accessions, which is enabling initial pangenomic analysis for some of the IWGC-selected 156 species. 157 As with accessibility of data, a core objective of the IWGC is to facilitate open access to

158 sequenced germplasm for all featured species. Historically, the weed science community has
159 rarely shared or adopted standard germplasm (e.g., specific weed accessions). The IWGC has

160 selected a specific accession of each species for reference genome assembly (typically 161 susceptible to herbicides). In collaboration with a parallel effort by the Herbicide Resistant Plants 162 committee of the Weed Science Society of America, seeds of the sequenced weed accessions 163 will be deposited in the United States Department of Agriculture Germplasm Resources 164 Information Network [22] for broad access by the scientific community. The IWGC ensures that 165 sequenced accessions are collected and documented to comply with the Nagoya Protocol on 166 access to genetic resources and the fair and equitable sharing of benefits arising from their 167 utilization under the Convention on Biological Diversity and related Access and Benefit Sharing 168 Legislation [23]. As additional accessions of weed species are sequenced (e.g., pangenomes are 169 obtained) the IWGC will facilitate germplasm sharing protocols to support collaboration. 170 Further, to simplify the investigation of herbicide resistance, the IWGC will link WeedPedia 171 with the International Herbicide-Resistant Weed Database [24], an already widely known and 172 utilized database for weed scientists.

173

174 Training and collaboration in weed genomics

Beyond producing genomic tools and resources, a priority of the IWGC is to enable the utilization of these resources across a wide range of stakeholders. A holistic approach to training is required for weed science generally [25], and we would argue even more so for weed genomics. To accomplish our training goals, the IWGC is developing and delivering programs aimed at the full range of IWGC stakeholders and covering a breadth of relevant topics. We have taken care to ensure our approaches are diverse as to provide training to researchers with all levels of existing experience and differing reasons for engaging with these tools. Throughout, the

focus is on ensuring that our training and outreach result in impacts that benefit a wide range ofstakeholders.

184 Although recently developed tools are incredibly enabling and have great potential to replace 185 antiquated methodology [26] and to solve pressing weed science problems [14], specialized 186 computational skills are required to fully explore and unlock meaning from these highly complex 187 datasets. Collaboration with, or training of, computational biologists equipped with these skills 188 and resources developed by the IWGC will enable weed scientists to expand research programs 189 and better understand the genetic underpinnings of weed evolution and herbicide resistance. To 190 fill existing skill gaps, the IWGC is developing summer bootcamps and online modules directed 191 specifically at weed scientists that will provide training on computational skills (Figure 1). 192 Because successful utilization of the IWGC resources requires more than general computational 193 skills, we have also created three additional targeted workshops that teach practical skills related 194 to genomics databases, molecular biology, and population genomics (available at [27]). 195 Engagement opportunities during undergraduate degrees has been shown to improve 196 academic outcomes [28, 29]. Therefore, the IWGC sponsors opportunities for undergraduates to 197 undertake 10-week Research Experiences for Undergraduates (REU). These REU include an 198 introduction to bioinformatics, a plant genomics research project that results in a presentation, 199 and access to career building opportunities in diverse workplace environments. To increase 200 equitable access to conferences and professional communities, we supported early career 201 researchers to attend the first two IWGC conferences in the USA as well as workshops and 202 bootcamps in Europe and South America. These hybrid or in-person travel grants are 203 intentionally designed to remove barriers and increase participation of individuals from 204 backgrounds and experiences currently underrepresented within weed/plant science or genomics

[30]. Recipients of these travel awards gave presentations and gained the measurable benefits
that come from either virtual or in-person participation in conferences [31]. Moving forward,
weed scientists must amass skills associated with genomic analyses and collaborate with other
area experts to fully leverage resources developed by the IWGC.

209

Evolution of Weediness: Potential Research Utilizing New Weed Genomics

211 **Tools**

212 Weeds can evolve from non-weed progenitors through wild colonization, crop de-

213 domestication, or crop-wild hybridization [32]. Because the time span in which weeds have

evolved is necessarily limited by the origins of agriculture, these non-weed relatives often still

exist and can be leveraged through population genomic and comparative genomic approaches to

216 identify the adaptive changes that have driven the evolution of weediness. The ability to rapidly

adapt, persist, and spread in agroecosystems are defining features of weedy plants, leading many

to advocate agricultural weeds as ideal candidates for studying rapid plant adaptation [33-36].

219 The insights gained from applying plant ecological approaches to the study of rapid weed

adaptation will move us towards the ultimate goals of mitigating such adaptation and increasing

the efficacy of crop breeding and biotechnology [14].

222

223 Biology and ecological genomics of weeds

The impressive community effort to create and maintain resources for *Arabidopsis thaliana* ecological genomics provides a motivating example for the emerging study of weed genomics [37-40]. *Arabidopsis thaliana* was the first flowering plant species to have its genome fully sequenced [41] and rapidly became a model organism for plant molecular biology. As weedy

228 genomes become available, collection, maintenance, and resequencing of globally distributed 229 accessions of these species will help to replicate the success found in ecological studies of A. 230 thaliana [42-48]. Evaluation of these accessions for traits of interest to produce large phenomics 231 data sets (as in [49-53]) enables genome-wide association studies and population genomics 232 analyses aimed at dissecting the genetic basis of variation in such traits [54]. Increasingly, these 233 resources (e.g the 1001 genomes project [42]) have enabled A. thaliana to be utilized as a model 234 species to explore the eco-evolutionary basis of plant adaptation in a more realistic ecological 235 context. Weedy species should supplement lessons in eco-evolutionary genomics learned from 236 these experiments in A. thaliana. 237 Untargeted genomic approaches for understanding the evolutionary trajectories of 238 populations and the genetic basis of traits as described above rely on the collection of genotypic 239 information from across the genome of many individuals. While whole-genome resequencing 240 accomplishes this requirement and requires no custom methodology, this approach provides 241 more information than is necessary and is prohibitively expensive in species with large genomes. 242 Development and optimization of genotype-by-sequencing methods for capturing reduced 243 representations of newly sequence genomes like those described by [55-57] will reduce the cost 244 and computational requirements of genetic mapping and population genetic experiments. 245 Additionally, the species sequenced by the IWGC do not currently have protocols for stable 246 transformation, a key development in the popularity of A. thaliana as a model organism and a 247 requirement for many functional genomic approaches. Functional validation of genes/variants 248 believed to be responsible for traits of interest in weeds has thus far relied on transiently 249 manipulating endogenous gene expression [58, 59] or ectopic expression of a transgene in a 250 model system [60-62]. While these methods have been successful, few weed species have well-

251 studied viral vectors to adapt for use in virus induced gene silencing and spray induced gene 252 silencing is relatively ineffective without the use of nanocarriers [63], which require specialized 253 equipment and expertise. Furthermore, traits with complex genetic architecture divergent 254 between the researched and model species may not be amenable to functional genomic 255 approaches using transgenesis techniques in model systems. Developing protocols for reduced 256 representation sequencing, stable transformation, and gene editing/silencing in weeds will allow 257 for more thorough characterization of candidate genetic variants underlying traits of interest. 258 Beyond rapid adaptation, some weedy species offer an opportunity to better understand co-259 evolution, like that between plants and pollinators and how their interaction leads to the spread of 260 weedy alleles (Table S1). A suite of plant-insect traits has co-evolved to maximize the attraction 261 of the insect pollinator community and the efficiency of pollen deposition between flowers 262 ensuring fruit and seed production in many weeds [64, 65]. Genetic mapping experiments have 263 identified genes and genetic variants responsible for many floral traits affecting pollinator 264 interaction including petal color [66-69], flower symmetry and size [70-72], and production of 265 volatile organic compounds [73-75] and nectar [76-78]. While these studies reveal candidate 266 genes for selection under co-evolution, herbicide resistance alleles may also have pleiotropic 267 effects on the ecology of weeds [79], altering plant-pollinator interactions [80]. Discovery of 268 genes and genetic variants involved in weed-pollinator interaction and their molecular and 269 environmental control may create opportunities for better management of weeds with insect-270 mediated pollination. For example, if management can disrupt pollinator attraction/interaction 271 with these weeds, the efficiency of reproduction may be reduced.

A more complete understanding of weed ecological genomics will undoubtedly elucidate
many unresolved questions regarding the genetic basis of various aspects of weediness. For

274 instance, when comparing populations of a species from agricultural and non-agricultural 275 environments, is there evidence for contemporary evolution of weedy traits selected by 276 agricultural management or were 'natural' populations pre-adapted to agroecosystems? Where 277 there is differentiation between weedy and natural populations, which traits are under selection 278 and what is the genetic basis of variation in those traits? When comparing between weedy 279 populations, is there evidence for parallel versus non-parallel evolution of weediness at the 280 phenotypic and genotypic levels? Such studies may uncover fundamental truths about weediness. 281 For example, is there a common phenotypic and/or genotypic basis for aspects of weediness 282 amongst diverse weed species? As genomic tools developed by the IWGC enable researchers to 283 address these questions, knowledge gained will help predict the potential development of newly 284 important weed species in new environments and cropping systems.

285

286 Population and Comparative Genomics

287 A fundamental attribute of locally adaptive genetic variation is that adaptive alleles are 288 overrepresented in their home environment relative to elsewhere [81]. This is a key motivation of 289 genotype-by-environment association (GEA) and selective sweep scan approaches, which allow 290 researchers to resolve the molecular basis of multi-dimensional adaptation [82, 83]. GEA 291 approaches, in particular, have been widely used on landscape-wide resequencing collections to 292 quantify the genetic basis of climate adaptation (e.g., [40, 84, 85]), but have yet to be fully 293 exploited to diagnose the genetic basis of the various aspects of weediness [86]. Armed with data 294 on environmental dimensions of agricultural settings, such as focal crop, soil quality, herbicide 295 use, and climate, GEA approaches can help disentangle how discrete farming practices have 296 influenced the evolution of weediness and resolve broader patterns of local adaptation across a

297 weed's range. Although non-weedy relatives are not technically required for GEA analyses, 298 inclusion of environmental and genomic data from weed progenitors can further distinguish 299 genetic variants underpinning weed origins from those involved in local adaptation. 300 Even without environmental or phenotypic data, the application of selective sweep scan 301 approaches to comparisons of weed and non-weed relatives facilitates powerful inference of 302 weed adaptation on micro- or macro-evolutionary scales. Two recent within-species examples 303 include weedy rice, where population differentiation between weedy and domesticated 304 populations was used to identify the genetic basis of weedy de-domestication [87], and common 305 waterhemp, where consistent allelic differences among natural and agricultural collections 306 resolved a complex set of agriculturally adaptive alleles [88, 89]. A recent comparative 307 population genomic study of weedy barnyardgrass and crop millet species has demonstrated how 308 inter-specific investigations can resolve the signatures of crop and weed evolution [90] (also see 309 [91] for a non-weed climate adaptation example). Multiple sequence alignments across numerous 310 species provide complementary insight into adaptive convergence over deeper timescales, even 311 with just one genomic sample per species (e.g., [92, 93]). Thus, the new IWGC weed genomes 312 combined with genomes available for closely related crops (outlined by [14, 94]) and an effort to 313 identify other non-weed wild relatives will be invaluable in characterizing the genetic 314 architecture of weed adaptation and evolution across diverse species.

315

316 *Herbicide resistance*

Herbicide resistance is among the numerous weedy traits that can evolve in plant populations
exposed to agricultural selection pressures. Over-reliance on herbicides to control weeds, along
with low diversity and lack of redundancy in weed management strategies, has resulted in

320 globally widespread herbicide resistance [95]. To date, 268 herbicide-resistant weed species have 321 been reported worldwide, and at least one resistance case exists for 21 of the 31 existing 322 herbicide sites of action [24] – significantly limiting chemical weed control options available to 323 agriculturalists. This limitation of control options is exacerbated by the recent lack of discovery 324 of herbicides with new sites of action [96]. 325 Herbicide resistance may result from several different physiological mechanisms. Such 326 mechanisms have been classified into two main groups, target-site resistance (TSR) [4, 97] and 327 non-target-site resistance (NTSR) [4, 98]. The first group encompasses changes that reduce 328 binding affinity between a herbicide and its target [99]. These changes may provide resistance to 329 multiple herbicides that have a common biochemical target [100] and can be effectively 330 managed through mixture and/or rotation of herbicides targeting different sites of action [101]. 331 The second group (NTSR), includes alterations in herbicide absorption, translocation, 332 sequestration, and/or metabolism that may lead to unpredictable pleotropic cross-resistance 333 profiles where structurally and functionally diverse herbicides are rendered ineffective by one or 334 more genetic variant(s) [60]. This mechanism of resistance threatens not only the efficacy of 335 existing herbicidal chemistries, but also ones yet to be discovered. While TSR is well understood 336 because of the ease of identification and molecular characterization of target site variants, NTSR 337 mechanisms are significantly more challenging to research because they are often polygenic, and 338 the resistance causing element(s) are not well understood [102]. 339 Improving the current understanding of metabolic NTSR mechanisms is not an easy task, 340 since genes of diverse biochemical functions are involved, many of which exist as extensive 341 gene families [100, 103]. Expression changes of NTSR genes have been implicated in several

342 resistance cases where the protein products of the genes are functionally equivalent across

343 sensitive and resistant plants, but their relative abundance leads to resistance. Thus, regulatory 344 elements of NTSR genes have been scrutinized to understand their role in NTSR mechanisms 345 [104]. Similarly, epigenetic modifications have been hypothesized to play a role in NTSR, with 346 much remaining to be explored [105-107]. Untargeted approaches such as genome-wide 347 association, selective sweep scans, linkage mapping, RNA-sequencing, and metabolomic 348 profiling have proven helpful to complement more specific biochemical- and chemo-349 characterization studies towards the elucidation of NTSR mechanisms as well as their regulation 350 and evolution [60, 108-115]. Due to their complexity and importance, the IWGC has begun 351 addressing this subject by manually curating the annotation of NTSR genes and developing a 352 standard nomenclature for the gene families often involved in NTSR. This standardization will 353 allow researchers to quickly identify true orthologous genes between weedy species, which is a 354 hurdle for current research of these complex and often vast gene families. 355 High-quality weed genome assemblies and gene model annotations have helped and will be 356 crucial for investigating the landscape of NTSR genes in weeds. They can also be used to predict 357 the protein structure for herbicide target site and metabolism genes to predict the efficacy and 358 selectivity of new candidate herbicides *in silico* to increase herbicide discovery throughput. 359 Knowledge of the genetic basis of NTSR will aid the rational design of herbicides by 1) 360 screening new compounds in the presence of newly discovered NTSR proteins during early 361 research phases; 2) identifying conserved chemical structures that interact with these proteins; 362 and 3) optimizing herbicide molecular design to lower potential for resistance evolution and 363 increase potency/spectrum of control. 364 Moving forward, genomic resources will be increasingly needed and used not only for the

design of conventional small molecule herbicides, but also for next generation technologies for

366 sustainable weed management. Proteolysis targeting chimeras (PROTACs) have the potential to 367 bind desired targets with great selectivity and degrade proteins by utilizing natural protein 368 ubiquitination and degradation pathways within plants [116]. The combination of nanoparticles 369 with oligonucleotides has recently shown potential to be used in spray applications towards gene 370 silencing in weeds, which paves the way for a new, innovative, and sustainable method for weed 371 management [117, 118]. Additionally, success in the field of pharmaceutical drug discovery in 372 the development of molecules modulating protein-protein interactions offers another potential 373 avenue towards the development of herbicides with novel targets [119, 120]. High-quality 374 genomic references allow for the design of new weed management technologies like the ones 375 listed here that are specific to – and effective across – weed species but have a null effect on non-376 target organisms. The tools being developed by the IWGC will have a crucial role in enabling the 377 development of next generation weed management strategies that will reduce our reliance on the 378 few chemical control options currently available to agriculturalists.

379

380 *Genome Biology*

381 The genomes of weed species are as diverse as weed species themselves. Many weed species 382 belong to unique plant families with no phylogenetically close model or crop species relatives for 383 comparison. On all measurable metrics, weed genomes run the gamut. Some have smaller 384 genomes like *Cyperus* spp. (~0.26 Gb) while others are larger, such as *Avena fatua* (~11.1 Gb) 385 (Table 1). Some have high heterozygosity in terms of single nucleotide polymorphisms, 386 repetitive DNA, and structural variants, such as the *Amaranthus* spp., while others are primarily self-pollinated and quite homozygous, such as Poa annua [121, 122]. Some are diploid such as 387 388 *Conyza canadensis* and *Echinochloa haploclada* while others are polyploid such as C.

sumetrensis, E. crus-galli, and *E. colona* [90]. The availability of genomic resources in these
diverse, unexplored branches of the tree of life allows us to identify consistencies and anomalies
in the field of genome biology.

392 The weed genomes published so far have focused mainly on weeds of agronomic crops, and 393 studies have revolved around their ability to resist key herbicides. For example, genomic 394 resources were vital in the elucidation of herbicide resistance cases involving target site gene 395 copy number variants (CNVs). Gene CNVs of 5-enolpyruvylshikimate-3-phosphate synthase 396 (EPSPS) have been found to confer resistance to the herbicide glyphosate in diverse weed 397 species. To date, nine species have independently evolved *EPSPS* CNVs, and species achieve 398 increased EPSPS copy number via different mechanisms [123]. For instance, the EPSPS CNV in 399 *Bassia scoparia* is caused by tandem duplication, which is accredited to transposable element 400 insertions flanking EPSPS and subsequent unequal crossing over events [124, 125]. In Eleusine 401 indica, a EPSPS CNV was caused by translocation of the EPSPS locus into the subtelomere 402 followed by telomeric sequence exchange [126]. One of the most fascinating genome biology 403 discoveries in weed science has been that of extra-chromosomal circular DNAs (eccDNAs) that 404 harbor the *EPSPS* gene in the weed species *Amaranthus palmeri* [127, 128]. In this case, the 405 eccDNAs autonomously replicate separately from the nuclear genome and do not reintegrate into 406 chromosomes, which has implications for inheritance, fitness, and genome structure [129]. These 407 discoveries would not have been possible without reference assemblies of weed genomes, next-408 generation sequencing, and collaboration with experts in plant genomics and bioinformatics. 409 Another question that is often explored with weedy genomes is the nature and composition of 410 gene families that are associated with NTSR. Gene families under consideration often include 411 cytochrome P450s (CYPs), glutathione-S-transferases (GSTs), ABC transporters, etc. Some

questions commonly considered with new weed genomes include: how many genes are in each
of these gene families, where are they located, and which weed accessions and species have an
over-abundance of them that might explain their ability to evolve resistance so rapidly [19, 90,
130, 131]? Weed genome resources are necessary to answer questions about gene family
expansion or contraction during the evolution of weediness, including the role of polyploidy in
NTSR gene family expansion as explored by [132].

418

419 Translational Research and Communication with Weed Management Stakeholders

420 Whereas genomics of model plants is typically aimed at addressing fundamental questions in 421 plant biology, and genomics of crop species has the obvious goal of crop improvement, goals of 422 genomics of weedy plants also include the development of more effective and sustainable 423 strategies for their management. Weed genomics assists with these objectives by providing novel 424 molecular ecological and evolutionary insights from the context of intensive anthropogenic 425 management (which is lacking in model plants), and offers knowledge and resources for trait 426 discovery for crop improvement, especially given that many wild crop relatives are also 427 important agronomic weeds (e.g. [133]). For instance, crop-wild relatives are valuable for 428 improving crop breeding for marginal environments [134]. Thus, weed genomics presents unique 429 opportunities and challenges relative to plant genomics more broadly. It should also be noted that 430 although weed science at its core is a very applied discipline, it draws broadly from many 431 scientific disciplines such as, plant physiology, chemistry, ecology, and evolutionary biology, to 432 name a few. The successful integration of weed-management strategies, therefore, requires 433 extensive collaboration among individuals collectively possessing the necessary expertise [135]. 434 Consequently, a major objective of the IWGC is to ensure that basic findings arising from weed

genomics are translated to advances in weed management and crop breeding by collaboratingbroadly with breeders, applied weed scientists, outreach specialists, and practitioners.

437 To accomplish this objective, the IWGC must facilitate communication of weed genomics 438 findings to relevant stakeholders (Figure 1). With the growing complexity of herbicide resistance 439 management, practitioners are beginning to recognize the importance of understanding resistance 440 mechanisms to inform appropriate management tactics [14]. Although weed science practitioners 441 do not need to understand the technical details of weed genomics, their appreciation of the power 442 of weed genomics - together with their unique insights from field observations - will yield novel 443 opportunities for applications of weed genomics to weed management. In particular, combining 444 field management history with information on weed resistance mechanisms is expected to 445 provide novel insights into evolutionary trajectories [e.g., 6, 136], which can be utilized for 446 disrupting evolutionary adaptation. It can be difficult to obtain field history information from 447 practitioners, but developing an understanding among them of the importance of such 448 information can be invaluable. To address these aspects, the IWGC can provide funding, or at 449 least coordinate teams, to build extension/education programs focused on weed genomics. 450 Factsheets and easy-to-understand infographics can be developed and communicated to various 451 stakeholders through traditional and electronic media.

452

453 **Conclusions**

Weeds are unique and fascinating plants, having significant impacts on agriculture and
ecosystems; and yet, aspects of their biology, ecology, and genetics remain poorly understood.
Weeds represent a unique area within plant biology, given their repeated rapid adaptation to
sudden and severe shifts in the selective landscape of anthropogenic management practices. The

458 production of a public genomics database with reference genomes for over 50 weed species 459 represents a substantial step forward towards research goals that improve our understanding of 460 the biology and evolution of weeds. Future work is needed to improve annotations, particularly 461 for complex gene families involved in herbicide detoxification, structural variants, and mobile 462 genetic elements, given the evidence to date of the generation of adaptive genetic variation in 463 weeds through structural variation. As reference genome assemblies become available; standard, 464 affordable methods for gathering genotype information will allow for the identification of 465 genetic variants underlying traits of interest. Further, development of methods for functional 466 gene validation and hypothesis testing is needed in weeds to validate the effect of genetic 467 variants detected through such experiments, including systems for transformation, gene editing, 468 and transient gene silencing and expression. Future research should focus on utilizing weed 469 genomes to investigate questions about the evolutionary biology, ecology, and genetics of weedy 470 traits and weed population dynamics. The IWGC plans to continue the public-private partnership 471 model to continue to host the WeedPedia database, integrate new datasets such as genome 472 resequencing and transcriptomes, conduct trainings, and serve as a research coordination 473 network to ensure that advances in weed science from around the world are shared across the 474 research community (Figure 1). Bridging basic plant genomics with translational applications in 475 weeds is needed to deliver on the potential of weed genomics to improve weed management and 476 crop breeding.

477

478 Availability of data and materials

The datasets supporting the conclusions of this article is included within the article and itsadditional files.

481

482 **Competing interests**

483 The authors declare that they have no competing interests.

484

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491 **References**

- 492 1. Gianessi LP, Nathan PR. The Value of Herbicides in U.S. Crop Production. Weed
- 493 Technol. 2007;21(2):559-66.
- 494 2. Pimentel D, Lach L, Zuniga R, Morrison D. Environmental and Economic Costs of
- 495 Nonindigenous Species in the United States. BioScience. 2000;50(1):53-65.
- 496 3. Barrett SH. Crop mimicry in weeds. Econ Bot. 1983;37(3):255-82.

497 4. Powles SB, Yu Q. Evolution in action: plants resistant to herbicides. Annu Rev Plant
498 Biol. 2010;61:317-47.

- 499 5. Thurber CS, Reagon M, Gross BL, Olsen KM, Jia Y, Caicedo AL. Molecular evolution
- of shattering loci in U.S. weedy rice. Mol Ecol. 2010;19(16):3271-84.
- 501 6. Comont D, Lowe C, Hull R, Crook L, Hicks HL, Onkokesung N, et al. Evolution of
- 502 generalist resistance to herbicide mixtures reveals a trade-off in resistance management. Nat
- 503 Commun. 2020;11(1):3086.

504	7.	Ashworth MB, Walsh MJ, Flower KC, Vila-Aiub MM, Powles SB. Directional selection
505	for flow	wering time leads to adaptive evolution in Raphanus raphanistrum (wild radish). Evol
506	Appl. 2	2016;9(4):619-29.
507	8.	Chan EK, Rowe HC, Kliebenstein DJ. Understanding the evolution of defense
508	metabo	olites in Arabidopsis thaliana using genome-wide association mapping. Genetics.
509	2010;1	85(3):991-1007.
510	9.	Frayling TM, Timpson NJ, Weedon MN, Zeggini E, Freathy RM, Lindgren CM, et al. A
511	commo	on variant in the FTO gene is associated with body mass index and predisposes to
512	childho	ood and adult obesity. Science. 2007;316(5826):889-94.
513	10.	Harkess A, Zhou J, Xu C, Bowers JE, Van der Hulst R, Ayyampalayam S, et al. The
514	asparag	gus genome sheds light on the origin and evolution of a young Y chromosome. Nat
515	Comm	un. 2017;8(1):1279.
516	11.	Periyannan S, Moore J, Ayliffe M, Bansal U, Wang X, Huang L, et al. The gene Sr33, an
517	ortholo	og of barley Mla genes, encodes resistance to wheat stem rust race Ug99. Science.
518	2013;3	41(6147):786-8.
519	12.	Ågren J, Oakley CG, McKay JK, Lovell JT, Schemske DW. Genetic mapping of
520	adapta	tion reveals fitness tradeoffs in Arabidopsis thaliana. Proc Natl Acad Sci U S A.
521	2013;1	10(52):21077-82.
522	13.	Schartl M, Walter RB, Shen Y, Garcia T, Catchen J, Amores A, et al. The genome of the
523	platyfi	sh, Xiphophorus maculatus, provides insights into evolutionary adaptation and several
524	comple	ex traits. Nat Genet. 2013;45(5):567-72.

525	14. Ravet K, Patterson EL, Krähmer H, Hamouzová K, Fan L, Jasieniuk M, et al. The power
526	and potential of genomics in weed biology and management. Pest Manag Sci. 2018;74(10):2216-
527	25.
528	15. Hufford MB, Seetharam AS, Woodhouse MR, Chougule KM, Ou S, Liu J, et al. <i>De novo</i>
529	assembly, annotation, and comparative analysis of 26 diverse maize genomes. Science.
530	2021;373(6555):655-62.

Liao W-W, Asri M, Ebler J, Doerr D, Haukness M, Hickey G, et al. A draft human
pangenome reference. Nature. 2023;617(7960):312-24.

533 17. Huang Y, Wu D, Huang Z, Li X, Merotto A, Bai L, et al. Weed genomics: yielding

insights into the genetics of weedy traits for crop improvement. aBIOTECH. 2023;4:20-30.

535 18. Bennetzen JL, Schmutz J, Wang H, Percifield R, Hawkins J, Pontaroli AC, et al.

536 Reference genome sequence of the model plant *Setaria*. Nat Biotechnol. 2012;30(6):555-61.

537 19. Kreiner JM, Giacomini DA, Bemm F, Waithaka B, Regalado J, Lanz C, et al. Multiple

538 modes of convergent adaptation in the spread of glyphosate-resistant Amaranthus tuberculatus.

539 Proc Natl Acad Sci U S A. 2019;116(42):21076-84.

540 20. Yu Y, Hu H, Doust AN, Kellogg EA. Divergent gene expression networks underlie

541 morphological diversity of abscission zones in grasses. New Phytol. 2020;225(4):1799-815.

542 21. International Weed Genomics Consortium Website. weedgenomics.org. Accessed 20543 June 2023.

544 22. USDA-ARS Germplasm Resources Information Network (GRIN). www.ars-grin.gov.
545 Accessed 20 June 2023.

546 23. Buck M, Hamilton C. The Nagoya Protocol on Access to Genetic Resources and the Fair
547 and Equitable Sharing of Benefits Arising from their Utilization to the Convention on Biological

548 Diversity. Review of European Community & International Environmental Law. 2011;20(1):47549 61.

550 24. The International Herbicide-Resistant Weed Database. www.weedscience.org. Accessed551 20 June 2023.

552 25. Chauhan BS, Matloob A, Mahajan G, Aslam F, Florentine SK, Jha P. Emerging

challenges and opportunities for education and research in weed science. Front Plant Sci.

554 2017;(8):1537.

555 26. Shah S, Lonhienne T, Murray CE, Chen Y, Dougan KE, Low YS, et al. Genome-Guided

556 Analysis of Seven Weed Species Reveals Conserved Sequence and Structural Features of Key

557 Gene Targets for Herbicide Development. Front Plant Sci. 2022;13:909073.

558 27. International Weed Genomics Consortium Training Resources.

www.weedgenomics.org/training-resources. Accessed 20 June 2023.

560 28. Blackford S. Harnessing the power of communities: career networking strategies for

561 bioscience PhD students and postdoctoral researchers. FEMS Microbiol Lett. 2018;365(8).

562 29. Pender M, Marcotte DE, Sto Domingo MR, Maton KI. The STEM Pipeline: The Role of

563 Summer Research Experience in Minority Students' Ph.D. Aspirations. Educ Policy Anal Arch.

564 2010;18(30):1-36.

30. Burke A, Okrent A, Hale K. The State of U.S. Science and Engineering 2022. National
Science Foundation. https://ncses.nsf.gov/pubs/nsb20221. 2022.

567 31. Wu J-Y, Liao C-H, Cheng T, Nian M-W. Using Data Analytics to Investigate Attendees'

568 Behaviors and Psychological States in a Virtual Academic Conference. Educ Technol Soc.

569 2021;24(1):75-91.

- 570 32. De Wet JMJ, Harlan JR. Weeds and domesticates: Evolution in the man-made habitat.
- 571 Econ Bot. 1975;29(2):99-108.
- 572 33. Mahaut L, Cheptou PO, Fried G, Munoz F, Storkey J, Vasseur F, et al. Weeds: Against
- 573 the Rules? Trends Plant Sci. 2020;25(11):1107-16.
- 574 34. Neve P, Vila-Aiub M, Roux F. Evolutionary-thinking in agricultural weed management.
- 575 New Phytol. 2009;184(4):783-93.
- 576 35. Sharma G, Barney JN, Westwood JH, Haak DC. Into the weeds: new insights in plant
- 577 stress. Trends Plant Sci. 2021;26(10):1050-60.
- 578 36. Vigueira CC, Olsen KM, Caicedo AL. The red queen in the corn: agricultural weeds as
- 579 models of rapid adaptive evolution. Heredity (Edinb). 2013;110(4):303-11.
- 580 37. Donohue K, Dorn L, Griffith C, Kim E, Aguilera A, Polisetty CR, et al. Niche
- 581 construction through germination cueing: life-history responses to timing of germination in
- 582 Arabidopsis thaliana. Evolution. 2005;59(4):771-85.
- 583 38. Exposito-Alonso M. Seasonal timing adaptation across the geographic range of
- 584 Arabidopsis thaliana. Proc Natl Acad Sci U S A. 2020;117(18):9665-67.
- 585 39. Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM. A map of
- local adaptation in *Arabidopsis thaliana*. Science. 2011;334(6052):86-9.
- 587 40. Hancock AM, Brachi B, Faure N, Horton MW, Jarymowycz LB, Sperone FG, et al.
- 588 Adaptation to climate across the *Arabidopsis thaliana* genome. Science. 2011;334(6052):83-6.
- 589 41. TAG Initiative. Analysis of the genome sequence of the flowering plant *Arabidopsis*
- *thaliana*. Nature. 2000;408(6814):796-815.

42. Alonso-Blanco C, Andrade J, Becker C, Bemm F, Bergelson J, Borgwardt KM, et al.
1,135 Genomes reveal the global pattern of polymorphism in *Arabidopsis thaliana*. Cell.
2016;166(2):481-91.

594 43. Durvasula A, Fulgione A, Gutaker RM, Alacakaptan SI, Flood PJ, Neto C, et al. African

595 genomes illuminate the early history and transition to selfing in Arabidopsis thaliana. Proc Natl

596 Acad Sci U S A. 2017;114(20):5213-18.

597 44. Frachon L, Mayjonade B, Bartoli C, Hautekèete N-C, Roux F. Adaptation to plant

communities across the genome of *Arabidopsis thaliana*. Mol Biol Evol. 2019;36(7):1442-56.

599 45. Fulgione A, Koornneef M, Roux F, Hermisson J, Hancock AM. Madeiran Arabidopsis

600 *thaliana* reveals ancient long-range colonization and clarifies demography in Eurasia. Mol Biol

601 Evol. 2018;35(3):564-74.

46. Fulgione A, Neto C, Elfarargi AF, Tergemina E, Ansari S, Göktay M, et al. Parallel

reduction in flowering time from *de novo* mutations enable evolutionary rescue in colonizing
lineages. Nat Commun. 2022;13(1):1461.

47. Kasulin L, Rowan BA, León RJC, Schuenemann VJ, Weigel D, Botto JF. A single

606 haplotype hyposensitive to light and requiring strong vernalization dominates Arabidopsis

thaliana populations in Patagonia, Argentina. Mol Ecol. 2017;26(13):3389-404.

48. Picó FX, Méndez-Vigo B, Martínez-Zapater JM, Alonso-Blanco C. Natural genetic

609 variation of *Arabidopsis thaliana* is geographically structured in the Iberian Peninsula. Genetics.

610 2008;180(2):1009-21.

611 49. Atwell S, Huang YS, Vilhjálmsson BJ, Willems G, Horton M, Li Y, et al. Genome-wide

612 association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. Nature.

613 2010;465(7298):627-31.

614 50. Flood PJ, Kruijer W, Schnabel SK, van der Schoor R, Jalink H, Snel JFH, et al.

- 615 Phenomics for photosynthesis, growth and reflectance in *Arabidopsis thaliana* reveals circadian
- and long-term fluctuations in heritability. Plant Methods. 2016;12(1):14.
- 617 51. Marchadier E, Hanemian M, Tisné S, Bach L, Bazakos C, Gilbault E, et al. The complex
- 618 genetic architecture of shoot growth natural variation in *Arabidopsis thaliana*. PLoS Genet.
- 619 2019;15(4):e1007954.
- 620 52. Tisné S, Serrand Y, Bach L, Gilbault E, Ben Ameur R, Balasse H, et al. Phenoscope: an
- automated large-scale phenotyping platform offering high spatial homogeneity. Plant J.
- 622 2013;74(3):534-44.
- 53. Tschiersch H, Junker A, Meyer RC, Altmann T. Establishment of integrated protocols for
 automated high throughput kinetic chlorophyll fluorescence analyses. Plant Methods.
- 625 2017;13:54.
- 626 54. Chen X, MacGregor DR, Stefanato FL, Zhang N, Barros-Galvão T, Penfield S. A VEL3
- 627 histone deacetylase complex establishes a maternal epigenetic state controlling progeny seed
- 628 dormancy. Nat Commun. 2023;14(1):2220.
- 629 55. Choi M, Scholl UI, Ji W, Liu T, Tikhonova IR, Zumbo P, et al. Genetic diagnosis by
- 630 whole exome capture and massively parallel DNA sequencing. Proc Natl Acad Sci U S A.
- 631 2009;106(45):19096-101.
- 632 56. Davey JW, Blaxter ML. RADSeq: next-generation population genetics. Brief Funct
 633 Genomics. 2010;9(5-6):416-23.
- 634 57. Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K, Buckler ES, et al. A robust,
- 635 simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS One.
- 636 2011;6(5):e19379.

637	58.	MacGregor DR. What makes a weed a weed? How virus-mediated reverse genetics can
638	help to	explore the genetics of weediness. Outlooks Pest Manag. 2020;31(5):224-29.
639	59.	Mellado-Sánchez M, McDiarmid F, Cardoso V, Kanyuka K, MacGregor DR. Virus-
640	media	ted transient expression techniques enable gene function studies in blackgrass. Plant
641	Physic	ol. 2020;183(2):455-59.
642	60.	Dimaano NG, Yamaguchi T, Fukunishi K, Tominaga T, Iwakami S. Functional
643	charac	terization of Cytochrome P450 CYP81A subfamily to disclose the pattern of cross-
644	resista	nce in <i>Echinochloa phyllopogon</i> . Plant Mol Biol. 2020;102(4-5):403-16.
645	61.	de Figueiredo MRA, Küpper A, Malone JM, Petrovic T, de Figueiredo ABTB,
646	Campa	agnola G, et al. An in-frame deletion mutation in the degron tail of auxin coreceptor IAA2
647	confer	s resistance to the herbicide 2,4-D in Sisymbrium orientale. Proc Natl Acad Sci U S A.
648	2022;1	19(9):e2105819119.
649	62.	Patzoldt WL, Hager AG, McCormick JS, Tranel PJ. A codon deletion confers resistance
650	to hert	picides inhibiting protoporphyrinogen oxidase. Proc Natl Acad Sci U S A.
651	2006;1	.03(33):12329-34.
652	63.	Schwartz SH, Hendrix B, Hoffer P, Sanders RA, Zheng W. Carbon dots for efficient
653	small	interfering RNA delivery and gene silencing in plants. Plant Physiol. 2020;184(2):647-57.
654	64.	Fattorini R, Glover BJ. Molecular mechanisms of pollination biology. Annu Rev Plant
655	Biol. 2	2020;71:487-515.
656	65.	Rollin O, Benelli G, Benvenuti S, Decourtye A, Wratten SD, Canale A, et al. Weed-
657	insect	pollinator networks as bio-indicators of ecological sustainability in agriculture. A review.
658	Agron	Sustain Dev. 2016;36(1):8.

- 659 66. Irwin RE, Strauss SY. Flower color microevolution in wild radish: evolutionary response
 660 to pollinator-mediated selection. Am Nat. 2005;165(2):225-37.
- 661 67. Ma B, Wu J, Shi T-L, Yang Y-Y, Wang W-B, Zheng Y, et al. Lilac (*Syringa oblata*)
- genome provides insights into its evolution and molecular mechanism of petal color change.
- 663 Commun Biol. 2022;5(1):686.
- 664 68. Xing A, Wang X, Nazir MF, Zhang X, Wang X, Yang R, et al. Transcriptomic and
- 665 metabolomic profiling of flavonoid biosynthesis provides novel insights into petals coloration in
- Asian cotton (*Gossypium arboreum* L.). BMC Plant Biol. 2022;22(1):416.
- 667 69. Zheng Y, Chen Y, Liu Z, Wu H, Jiao F, Xin H, et al. Important roles of key genes and
- transcription factors in flower color differences of *Nicotianaalata*. Genes (Basel).
- **669** 2021;12(12):1976.
- 670 70. Krizek BA, Anderson JT. Control of flower size. J Exp Bot. 2013;64(6):1427-37.
- 671 71. Powell AE, Lenhard M. Control of organ size in plants. Curr Biol. 2012;22(9):R360-7.
- 672 72. Spencer V, Kim M. Re"CYC"ling molecular regulators in the evolution and development
- 673 of flower symmetry. Semin Cell Dev Biol. 2018;79:16-26.
- 674 73. Amrad A, Moser M, Mandel T, de Vries M, Schuurink RC, Freitas L, et al. Gain and loss
- 675 of floral scent production through changes in structural genes during pollinator-mediated
- 676 speciation. Curr Biol. 2016;26(24):3303-12.
- 677 74. Delle-Vedove R, Schatz B, Dufay M. Understanding intraspecific variation of floral scent
- 678 in light of evolutionary ecology. Ann Bot. 2017;120(1):1-20.
- 679 75. Pichersky E, Gershenzon J. The formation and function of plant volatiles: perfumes for
- 680 pollinator attraction and defense. Curr Opin Plant Biol. 2002;5(3):237-43.

- 681 76. Ballerini ES, Kramer EM, Hodges SA. Comparative transcriptomics of early petal
- 682 development across four diverse species of *Aquilegia* reveal few genes consistently associated
- 683 with nectar spur development. BMC Genom. 2019;20(1):668.
- 684 77. Corbet SA, Willmer PG, Beament JWL, Unwin DM, Prys-Jones OE. Post-secretory
- determinants of sugar concentration in nectar. Plant Cell Environ. 1979;2(4):293-308.
- 686 78. Galliot C, Hoballah ME, Kuhlemeier C, Stuurman J. Genetics of flower size and nectar
- volume in petunia pollination syndromes. Planta. 2006;225(1):203-12.
- 688 79. Vila-Aiub MM, Neve P, Powles SB. Fitness costs associated with evolved herbicide
- resistance alleles in plants. New Phytol. 2009;184(4):751-67.
- 690 80. Baucom RS. Evolutionary and ecological insights from herbicide-resistant weeds: what
- have we learned about plant adaptation, and what is left to uncover? New Phytol.
- **692** 2019;223(1):68-82.
- 693 81. Kawecki TJ, Ebert D. Conceptual issues in local adaptation. Ecol Lett. 2004;7(12):1225694 41.
- 69582.Lasky JR, Josephs EB, Morris GP. Genotype–environment associations to reveal the
- 696 molecular basis of environmental adaptation. Plant Cell. 2023;35(1):125-38.
- 697 83. Lotterhos KE. The effect of neutral recombination variation on genome scans for
- 698 selection. G3-Genes Genom Genet. 2019;9(6):1851-67.
- 699 84. Lovell JT, MacQueen AH, Mamidi S, Bonnette J, Jenkins J, Napier JD, et al. Genomic
- 700 mechanisms of climate adaptation in polyploid bioenergy switchgrass. Nature.
- 701 2021;590(7846):438-44.
- 702 85. Todesco M, Owens GL, Bercovich N, Légaré J-S, Soudi S, Burge DO, et al. Massive
- haplotypes underlie ecotypic differentiation in sunflowers. Nature. 2020;584(7822):602-07.

704	86.	Revolinski SR, Maughan PJ, Coleman CE, Burke IC. Preadapted to adapt: Underpinnings
705	of ad	ptive plasticity revealed by the downy brome genome. Commun Biol. 2023;6:326.

706 87. Qiu J, Zhou Y, Mao L, Ye C, Wang W, Zhang J, et al. Genomic variation associated with

local adaptation of weedy rice during de-domestication. Nat Commun. 2017;8(1):15323.

708 88. Kreiner JM, Caballero A, Wright SI, Stinchcombe JR. Selective ancestral sorting and de

novo evolution in the agricultural invasion of *Amaranthus tuberculatus*. Evolution.

710 2022;76(1):70-85.

711 89. Kreiner JM, Latorre SM, Burbano HA, Stinchcombe JR, Otto SP, Weigel D, et al. Rapid

712 weed adaptation and range expansion in response to agriculture over the past two centuries.

713 Science. 2022;378(6624):1079-85.

714 90. Wu D, Shen E, Jiang B, Feng Y, Tang W, Lao S, et al. Genomic insights into the

evolution of *Echinochloa* species as weed and orphan crop. Nat Commun. 2022;13(1):689.

716 91. Yeaman S, Hodgins KA, Lotterhos KE, Suren H, Nadeau S, Degner JC, et al. Convergent

local adaptation to climate in distantly related conifers. Science. 2016;353(6306):1431-33.

718 92. Haudry A, Platts AE, Vello E, Hoen DR, Leclercq M, Williamson RJ, et al. An atlas of

over 90,000 conserved noncoding sequences provides insight into crucifer regulatory regions.

720 Nat Genet. 2013;45(8):891-98.

721 93. Sackton TB, Grayson P, Cloutier A, Hu Z, Liu JS, Wheeler NE, et al. Convergent

regulatory evolution and loss of flight in paleognathous birds. Science. 2019;364(6435):74-78.

723 94. Ye CY, Fan L. Orphan crops and their wild relatives in the genomic era. Mol Plant.

724 2021;14(1):27-39.

725 95. Bourguet D, Delmotte F, Franck P, Guillemaud T, Reboud X, Vacher C, et al.

Heterogeneity of selection and the evolution of resistance. Trends Ecol Evol. 2013;28(2):110-8.

727 96. Powles S. Herbicide discovery through innovation and diversity. Adv Weed Sci.

- 728 2022;40(spe1): e020220074.
- 729 97. Murphy BP, Tranel PJ. Target-site mutations conferring herbicide resistance. Plants
- 730 (Basel). 2019;8(10):382.
- 731 98. Gaines TA, Duke SO, Morran S, Rigon CAG, Tranel PJ, Küpper A, et al. Mechanisms of
- evolved herbicide resistance. J Biol Chem. 2020;295(30):10307-30.
- 733 99. Lonhienne T, Cheng Y, Garcia MD, Hu SH, Low YS, Schenk G, et al. Structural basis of
- resistance to herbicides that target acetohydroxyacid synthase. Nat Commun. 2022;13(1):3368.
- 100. Comont D, MacGregor DR, Crook L, Hull R, Nguyen L, Freckleton RP, et al. Dissecting
- 736 weed adaptation: Fitness and trait correlations in herbicide-resistant *Alopecurus myosuroides*.
- 737 Pest Manag Sci. 2022;78(7):3039-50.
- 101. Neve P. Simulation modelling to understand the evolution and management of glyphosate
- resistance in weeds. Pest Manag Sci. 2008;64(4):392-401.
- 740 102. Torra J, Alcántara-de la Cruz R. Molecular mechanisms of herbicide resistance in weeds.
- 741 Genes (Basel). 2022;13(11):2025.
- 103. Délye C, Gardin JAC, Boucansaud K, Chauvel B, Petit C. Non-target-site-based
- resistance should be the centre of attention for herbicide resistance research: *Alopecurus*
- *myosuroides* as an illustration. Weed Res. 2011;51(5):433-37.
- 745 104. Chandra S, Leon RG. Genome-wide evolutionary analysis of putative non-specific
- herbicide resistance genes and compilation of core promoters between monocots and dicots.
- 747 Genes (Basel). 2022;13(7):1171.
- 748 105. Margaritopoulou T, Tani E, Chachalis D, Travlos I. Involvement of epigenetic
- mechanisms in herbicide resistance: The case of *Conyza canadensis*. Agriculture. 2018;8(1):17.

- 750 106. Pan L, Guo Q, Wang J, Shi L, Yang X, Zhou Y, et al. CYP81A68 confers metabolic
- resistance to ALS and ACCase-inhibiting herbicides and its epigenetic regulation in *Echinochloa*
- 752 *crus-galli*. J Hazard Mater. 2022;428:128225.
- 753 107. Sen MK, Hamouzová K, Košnarová P, Roy A, Soukup J. Herbicide resistance in grass
- weeds: Epigenetic regulation matters too. Front Plant Sci. 2022;13:1040958.
- 108. Han H, Yu Q, Beffa R, González S, Maiwald F, Wang J, et al. Cytochrome P450
- 756 *CYP81A10v7* in *Lolium rigidum* confers metabolic resistance to herbicides across at least five
- 757 modes of action. Plant J. 2021;105(1):79-92.
- 758 109. Kubis GC, Marques RZ, Kitamura RS, Barroso AA, Juneau P, Gomes MP. Antioxidant
- enzyme and Cytochrome P450 activities are involved in horseweed (*Conyza sumatrensis*)
- resistance to glyphosate. Stress. 2023;3(1):47-57.
- 761 110. Qiao Y, Zhang N, Liu J, Yang H. Interpretation of ametryn biodegradation in rice based
- on joint analyses of transcriptome, metabolome and chemo-characterization. J Hazard Mater.

763 2023;445:130526.

- 764 111. Rouse CE, Roma-Burgos N, Barbosa Martins BA. Physiological assessment of non-
- target site resistance in multiple-resistant junglerice (*Echinochloa colona*). Weed Sci.

766 2019;67(6):622-32.

- 767 112. Abou-Khater L, Maalouf F, Jighly A, Alsamman AM, Rubiales D, Rispail N, et al.
- 768 Genomic regions associated with herbicide tolerance in a worldwide faba bean (*Vicia faba* L.)
- 769 collection. Sci Rep. 2022;12(1):158.
- 113. Gupta S, Harkess A, Soble A, Van Etten M, Leebens-Mack J, Baucom RS.
- 771 Interchromosomal linkage disequilibrium and linked fitness cost loci associated with selection
- for herbicide resistance. New Phytol. 2023;238(3):1263-77.

773	114. Kreiner JM, Tranel PJ, Weigel D, Stinchcombe JR, Wright SI. The genetic architecture
774	and population genomic signatures of glyphosate resistance in Amaranthus tuberculatus. Mol
775	Ecol. 2021;30(21):5373-89.
776	115. Parcharidou E, Dücker R, Zöllner P, Ries S, Orru R, Beffa R. Recombinant glutathione
777	transferases from flufenacet-resistant black-grass (Alopecurus myosuroides Huds.) form different
778	flufenacet metabolites and differ in their interaction with pre- and post-emergence herbicides.
779	Pest Manag Sci. 2023;in press.
780	116. Békés M, Langley DR, Crews CM. PROTAC targeted protein degraders: the past is
781	prologue. Nat Rev Drug Discov. 2022;21(3):181-200.
782	117. Martin K, Gaines T, Aishwarya V. Pairing nanoparticles with FANA technology for
783	spray-on gene silencing in weeds. Weed Science Society of America Annual Meeting; Arlington,
784	VA. 2023.
785	118. Zabala-Pardo D, Gaines T, Lamego FP, Avila LA. RNAi as a tool for weed management:
786	challenges and opportunities. Adv Weed Sci. 2022;40(spe1): e020220096.
787	119. Acuner Ozbabacan SE, Engin HB, Gursoy A, Keskin O. Transient protein-protein
788	interactions. Protein Eng Des Sel. 2011;24(9):635-48.
789	120. Lu H, Zhou Q, He J, Jiang Z, Peng C, Tong R, et al. Recent advances in the development
790	of protein-protein interactions modulators: mechanisms and clinical trials. Signal Transduct
791	Target Ther. 2020;5(1):213.
792	121. Benson CW, Sheltra MR, Maughan PJ, Jellen EN, Robbins MD, Bushman BS, et al.
793	Homoeologous evolution of the allotetraploid genome of Poa annua L. BMC Genom.
794	2023;24(1):350.

- 122. Robbins MD, Bushman BS, Huff DR, Benson CW, Warnke SE, Maughan CA, et al.
- 796 Chromosome-scale genome assembly and annotation of allotetraploid annual bluegrass (Poa
- 797 *annua* L.). Genome Biol Evol. 2022;15(1):evac180.
- 123. Patterson EL, Pettinga DJ, Ravet K, Neve P, Gaines TA. Glyphosate resistance and
- 799 EPSPS gene duplication: Convergent evolution in multiple plant species. J Hered.
- 800 2018;109(2):117-25.
- 801 124. Jugulam M, Niehues K, Godar AS, Koo DH, Danilova T, Friebe B, et al. Tandem
- amplification of a chromosomal segment harboring 5-enolpyruvylshikimate-3-phosphate
- 803 synthase locus confers glyphosate resistance in *Kochia scoparia*. Plant Physiol.
- 804 2014;166(3):1200-7.
- 805 125. Patterson EL, Saski CA, Sloan DB, Tranel PJ, Westra P, Gaines TA. The draft genome of
- 806 *Kochia scoparia* and the mechanism of glyphosate resistance via transposon-mediated *EPSPS*
- tandem gene duplication. Genome Biol Evol. 2019;11(10):2927-40.
- 808 126. Zhang C, Johnson N, Hall N, Tian X, Yu Q, Patterson E. Subtelomeric 5-
- 809 enolpyruvylshikimate-3-phosphate synthase (EPSPS) copy number variation confers glyphosate
- 810 resistance in *Eleusine indica*. Res Sq. 2023;rs.3.rs-2587355.
- 811 127. Koo D-H, Molin WT, Saski CA, Jiang J, Putta K, Jugulam M, et al. Extrachromosomal
- 812 circular DNA-based amplification and transmission of herbicide resistance in crop weed
- 813 *Amaranthus palmeri*. Proc Natl Acad Sci U S A. 2018;115(13):3332-37.
- 814 128. Molin WT, Yaguchi A, Blenner M, Saski CA. The eccDNA replicon: A heritable,
- 815 extranuclear vehicle that enables gene amplification and glyphosate resistance in *Amaranthus*
- 816 *palmeri*. Plant Cell. 2020;32(7):2132-40.

- 817 129. Jugulam M. Can non-Mendelian inheritance of extrachromosomal circular DNA-
- 818 mediated EPSPS gene amplification provide an opportunity to reverse resistance to glyphosate?
- 819 Weed Res. 2021;61(2):100-05.
- 820 130. Wang L, Sun X, Peng Y, Chen K, Wu S, Guo Y, et al. Genomic insights into the origin,
- adaptive evolution, and herbicide resistance of *Leptochloa chinensis*, a devastating tetraploid
- 822 weedy grass in rice fields. Mol Plant. 2022;15(6):1045-58.
- 823 131. Cai L, Comont D, MacGregor D, Lowe C, Beffa R, Neve P, et al. The blackgrass genome
- 824 reveals patterns of non-parallel evolution of polygenic herbicide resistance. New Phytol.
- 825 2023;237(5):1891-907.
- 826 132. Chen K, Yang H, Peng Y, Liu D, Zhang J, Zhao Z, et al. Genomic analyses provide
- 827 insights into the polyploidization-driven herbicide adaptation in *Leptochloa* weeds. Plant
- Biotechnol J. 2023; in press.
- 829 133. Ohadi S, Hodnett G, Rooney W, Bagavathiannan M. Gene flow and its consequences in
 830 *Sorghum spp.* Crit Rev Plant Sci. 2017;36(5-6):367-85.
- 831 134. Renzi JP, Coyne CJ, Berger J, von Wettberg E, Nelson M, Ureta S, et al. How could the
- use of crop wild relatives in breeding increase the adaptation of crops to marginal environments?
- 833 Front Plant Sci. 2022;13;886162.
- 834 135. Ward SM, Cousens RD, Bagavathiannan MV, Barney JN, Beckie HJ, Busi R, et al.
- Agricultural weed research: A critique and two proposals. Weed Sci. 2014;62(4):672-78.
- 836 136. Evans JA, Tranel PJ, Hager AG, Schutte B, Wu C, Chatham LA, et al. Managing the
- evolution of herbicide resistance. Pest Management Science. 2016;72(1):74-80.

838 137. Montgomery JS, Giacomini D, Waithaka B, Lanz C, Murphy BP, Campe R, et	et al. Draft	. et a	ampe R.	. Cam	v BP.	<i>Aurphy</i>	Mu	nz C.	. L	Waithaka I	D.	Giacomini	JS.	Montgomer	137.	838
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- 839 genomes of Amaranthus tuberculatus, Amaranthus hybridus and Amaranthus palmeri. Genome
- Biol Evol. 2020;12:1988-93.
- 138. Jeschke MR, Tranel PJ, Rayburn AL. DNA content analysis of smooth pigweed
- 842 (Amaranthus hybridus) and tall waterhemp (A. tuberculatus): implications for hybrid detection.
- 843 Weed Sci. 2003;51(1):1-3.
- 844 139. Rayburn AL, McCloskey R, Tatum TC, Bollero GA, Jeschke MR, Tranel PJ. Genome
- size analysis of weedy *Amaranthus* species. Crop Sci. 2005;45(6):2557-62.
- 846 140. Mulligan GA. Chromosome numbers of Canadian weeds. I. Canad J Bot.
- 847 1957;35(5):779-89.
- 848 141. Meyer L, Causse R, Pernin F, Scalone R, Bailly G, Chauvel B, et al. New gSSR and
- 849 EST-SSR markers reveal high genetic diversity in the invasive plant Ambrosia artemisiifolia L.
- and can be transferred to other invasive *Ambrosia* species. PLOS ONE. 2017;12(5):e0176197.
- 851 142. Pustahija F, Brown SC, Bogunić F, Bašić N, Muratović E, Ollier S, et al. Small genomes
- dominate in plants growing on serpentine soils in West Balkans, an exhaustive study of 8
- 853 habitats covering 308 taxa. Plant Soil. 2013;373(1):427-53.
- 854 143. Kubešová M, Moravcova L, Suda J, Jarošík V, Pyšek P. Naturalized plants have smaller
- genomes than their non-invading relatives: a flow cytometric analysis of the Czech alien flora.
- 856 Preslia. 2010;82(1):81-96.
- 857 144. Thébaud C, Abbott RJ. Characterization of invasive Conyza species (Asteraceae) in
- Europe: Quantitative trait and isozyme analysis. Am J Bot. 1995;82(3):360-68.

- 859 145. Garcia S, Hidalgo O, Jakovljević I, Siljak-Yakovlev S, Vigo J, Garnatje T, et al. New
- data on genome size in 128 Asteraceae species and subspecies, with first assessments for 40
- genera, 3 tribes and 2 subfamilies. Plant Biosyst. 2013;147(4):1219-27.
- 862 146. Bennett MD, Leitch IJ, Hanson L. DNA amounts in two samples of angiosperm weeds.
- 863 Ann Bot. 1998;82:121-34.
- 864 147. Schulz-Schaeffer J, Gerhardt S. Cytotaxonomic analysis of the Euphorbia spp. (leafy
- spurge) complex. II: Comparative study of the chromosome morphology. Biol Zentralbl.
- 866 1989;108(1):69-76.
- 867 148. Schaeffer JR, Gerhardt S. The impact of introgressive hybridization on the weediness of
- leafy spurge. 1989 Leafy Spurge Symposium. 1989: 97-105.
- 869 149. Bai C, Alverson WS, Follansbee A, Waller DM. New reports of nuclear DNA content for
- 407 vascular plant taxa from the United States. Ann Bot. 2012;110(8):1623-29.
- 871 150. Aarestrup JR, Karam D, Fernandes GW. Chromosome number and cytogenetics of
- 872 *Euphorbia heterophylla* L. Genet Mol Res. 2008;7(1):217-22.
- 873 151. Wang L, Sun X, Peng Y, Chen K, Wu S, Guo Y, et al. Genomic insights into the origin,
- adaptive evolution, and herbicide resistance of *Leptochloa chinensis*, a devastating tetraploid
- weedy grass in rice fields. Molecular Plant. 2022;15(6):1045-58.
- 876 152. Paril J, Pandey G, Barnett EM, Rane RV, Court L, Walsh T, et al. Rounding up the
- 877 annual ryegrass genome: High-quality reference genome of *Lolium rigidum*. Front Genet.
- 878 2022;13:1012694.
- 879 153. Weiss-Schneeweiss H, Greilhuber J, Schneeweiss GM. Genome size evolution in
- holoparasitic *Orobanche* (Orobanchaceae) and related genera. Am J Bot. 2006;93(1):148-56.

	Lez E, Bennett F, Subba Rao P. Biology & chemistry of	nell J. Rodriguez E	Towers G. Mitchell	881 154.
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- 882 *Parthenium hysterophorus* L., a problem weed in India. Biol Rev. 1977;48:65-74.
- 883 155. Moghe GD, Hufnagel DE, Tang H, Xiao Y, Dworkin I, Town CD, et al. Consequences of
- 884 whole-genome triplication as revealed by comparative genomic analyses of the wild radish
- (*Raphanus raphanistrum*) and three other Brassicaceae species. Plant Cell. 2014;26(5):1925-37.
- 886 156. Zhang X, Liu T, Wang J, Wang P, Qiu Y, Zhao W, et al. Pan-genome of Raphanus
- highlights genetic variation and introgression among domesticated, wild, and weedy radishes.
- 888 Mol Plant. 2021;14(12):2032-55.
- 889 157. Chytrý M, Danihelka J, Kaplan Z, Wild J, Holubová D, Novotný P, et al. Pladias
- database of the Czech flora and vegetation. Preslia. 2021;93(1):1-87.
- 891 158. Kersten S, Chang J, Huber CD, Voichek Y, Lanz C, Hagmaier T, et al. Standing genetic
- 892 variation fuels rapid evolution of herbicide resistance in blackgrass. Proc Natl Acad Sci U S A.
- 893 2023;120(16):e2206808120.
- 159. Chen J, Hall N, Saski C, Westra P, Gaines T, Patterson EL. FHY3/FAR1 transposable
- elements generate adaptive genetic variation in the *Bassia scoparia* genome. bioRxiv. 2023;
- 896 DOI:10.1101/2023.05.26.542497.
- 897 160. Jarvis DE, Sproul JS, Navarro-Domínguez B, Krak K, Jaggi K, Huang Y-F, et al.
- 898 Chromosome-scale genome assembly of the hexaploid Taiwanese goosefoot "Djulis"
- 899 (*Chenopodium formosanum*). Genome Biol Evol. 2022;14(8):evac120.
- 900 161. Laforest M, Martin SL, Bisaillon K, Soufiane B, Meloche S, Page E. A chromosome-
- scale draft sequence of the Canada fleabane genome. Pest Manag Sci. 2020;76:2158-69.

902	162. Guo L, Qiu J, Ye C, Jin G, Mao L, Zhang H, et al. Echinochloa crus-galli genome	
903	analysis provides insight into its adaptation and invasiveness as a weed. Nat Commun.	
904	2017;8(1):1031.	

- 905 163. Sun J, Ma D, Tang L, Zhao M, Zhang G, Wang W, et al. Population genomic analysis
- and *de novo* assembly reveal the origin of weedy rice as an evolutionary game. Mol Plant.

907 2019;12(5):632-47.

- 908 164. Mao Q, Huff DR. The evolutionary origin of *Poa annua* L. Crop Sci. 2012;52(4):1910909 22.
- 910 165. Benson CW, Sheltra MR, Maughan JP, Jellen EN, Robbins MD, Bushman BS, et al.
- 911 Homoeologous evolution of the allotetraploid genome of *Poa annua* L. Res Sq. 2023;DOI:
- 912 10.21203/rs.3.rs-2729084/v1.
- 913 166. Thielen PM, Pendleton AL, Player RA, Bowden KV, Lawton TJ, Wisecaver JH.
- 914 Reference genome for the highly transformable *Setaria viridis* ME034V. G3 (Bethesda, Md).
 915 2020;10(10):3467-78.
- 916 167. Yoshida S, Kim S, Wafula EK, Tanskanen J, Kim Y-M, Honaas L, et al. Genome
- 917 sequence of *Striga asiatica* provides insight into the evolution of plant parasitism. Curr Biol.
 918 2019;29(18):3041-52.e4.
- 919 168. Qiu S, Bradley JM, Zhang P, Chaudhuri R, Blaxter M, Butlin RK, et al. Genome-enabled
- 920 discovery of candidate virulence loci in *Striga hermonthica*, a devastating parasite of African
- 921 cereal crops. New Phytol. 2022;236(2):622-38.
- 922 169. Nunn A, Rodríguez-Arévalo I, Tandukar Z, Frels K, Contreras-Garrido A, Carbonell-
- 923 Bejerano P, et al. Chromosome-level *Thlaspi arvense* genome provides new tools for

- translational research and for a newly domesticated cash cover crop of the cooler climates. Plant
- 925 Biotechnol J. 2022;20(5):944-63.
- 926
- Table 1. Genome assemblies of 31 weed species completed or ongoing by the International
- 928 Weed Genomics Consortium.

Scientific name	Common name	Haplotypes in Assembly	Public Availability Ploidy Date		X	n	Genome Size Estimate (Gbp)
Amaranthus hybridus	smooth pigweed	1; Previous version [137]	September 2023 diploid		16	16	0.509 [138]
Amaranthus palmeri	Palmer amaranth	Previous version [137]	June 2024 diploid		17	17	0.445 [139]
Amaranthus retroflexus	redroot pigweed		In progress diploid		16	16	0.592 [139]
Amaranthus tuberculatus	common waterhemp	2; Previous version [137]	November 2023 diploid		16	16	0.694 [139]
Ambrosia artemisiifolia	common ragweed		In progress	diploid [140, 141]	18	18	1.152 [142]
Ambrosia trifida	giant ragweed		December 2023	diploid [140]	12	12	1.872 [143]
Apera spica- venti	loose silkybent	2	August 2023	diploid	7	7	4.622
Avena fatua	wild oat	1	August 2023 hexaploid (Additional file 1)		7	21	11.248
Chenopodium album	common lambsquarters	1	July 2023	hexaploid	9	27	1.59

Cirsium arvense	Canada thistle		In progress	diploid	17	17	1.415
Convolvulus arvensis	field bindweed		In progress	diploid ⁺	12+	12+	0.652 [142]
Conyza bonariensis (Erigeron bonariensis)	hairy fleabane		In progress	hexaploid [144]	9	27	2.043 [145]
Conyza sumatrensis (Erigeron sumatrensis)	Sumatran fleabane	1	May 2023	hexaploid	9	27	1.874
Cyperus esculentus	yellow nutsedge	2	July 2023	diploid	54	54	0.588 [146]
Cyperus rotundus	purple nutsedge	2	December 2023	diploid	54	54	0.49 [146]
Digitaria insularis	sourgrass	1	September 2023	tetraploid	9	18	1.529
Digitaria ischaemum	hairy crabgrass		In progress	tetraploid	9	18	Unknown, in progress
Echinochloa colona	junglerice (weedy genotype)	See crop genotype assembly by [90]	In progress	hexaploid	9	27	1.372 [146]
Euphorbia esula	leafy spurge		In progress	hexaploid ⁺ [based on 147, 148]	10+	60 ⁺	2.3 [149]
Euphorbia heterophylla	wild poinsettia		July 2024	diploid [150]	14	14	Unknown, in progress
Leptochloa chinensis	Chinese sprangletop	2; See also [151]	August 2023	diploid	10	10	0.454
Lolium rigidum	annual ryegrass	2; See also [152]	August 2023	diploid (Additional file 1)	7	7	2.41

Orobanche cernua	nodding broomrape		In progress	diploid	19	19	1.421 [153]
Orobanche crenata	crenate broomrape		In progress	diploid	19	19	2.787 [153]
Orobanche minor	small broomrape		In progress	diploid	19	19	1.792 [153]
Parthenium hysterophorus	ragweed parthenium		In progress	diploid [154]	17	17	Unknown, in progress
Phalaris minor	little seed canary grass	1	August 2023	tetraploid (Additional file 1)	7	14	5.851
Raphanus raphanistrum	wild radish	Previous versions [155, 156]	In progress	diploid	9	9	0.515 [155]
Salsola tragus	Russian thistle	2	July 2023	tetraploid (Additional file 1)	9	18	1.319
*Sorghum halepense	johnsongrass	2	September 2023	tetraploid	10	20	1.752
Verbascum blattaria	moth mullein	1	December 2023	diploid	15	15	0.344 [157]

929

Table 1. Genome assemblies of 31 weed species completed or ongoing by the International

931 Weed Genomics Consortium. All completed genomes are platinum assembly quality, defined as

having chromosome-length scaffolds (i.e., 1-3 scaffolds per chromosome) for the assembly,

933 unless indicated by *. Genome size estimated from flow cytometry or published references as

indicated. + indicates that verification is currently in progress for cytogenetic information.

935

Table 2. Genomic information for 19 weed species produced without assistance by the

937 International Weed Genomics Consortium.

Scientific name	Common name	v	n	1n Genome Size	Genome Assembly
Scientific fiame	Common name	х	n	Estimate (Gbp)	Size (Gbp)
Alopecurus	blaskerass	7	7	2 56 [159]	3.4-3.56 [131,
myosuroides	blackgrass	/	/	3.56 [158]	158]
Bassia scoparia	kochia	9	9	0.969 [159]	0.970 [159]
Bromus tectorum	cheatgrass	7	7		2.48 [86]
Chenopodium					
formosanum					
(domesticated	Djulis	9	27	1.69 [160]	1.59 [160]
genotype of C.					
album)					
Conyza	horseweed	9	9	0.425 [161]	0.426 [161]
canadensis	noiseweed)	0.425 [101]	0.420 [101]
Echinochloa					
colona (crop	junglerice	9	27	1.18 [90]	1.13 [90]
genotype)					
Echinochloa crus-	barnyardgrass	9	27	1.4 [162]	1.34 [90]
galli	ounijulugiuss	,	27	1.1 [102]	1.5 [[7 0]
Echinochloa					
oryzicola (syn. E.	late watergrass	9	18	1.0 [162]	0.95 [90]
phyllopogon)					
Eleusine indica	goosegrass	9	9		0.510 [126]
Ipomoea purpurea	common	15	15	0.81 [113]	0.60 [113]

	morning-glory				
Lolium perenne	perennial ryegrass	7	7		2.63 (Bushman and Robbins, pers. comm.)
Oryza sativa f. spontanea	weedy rice	12	12		0.37 [163]
Poa annua	annual bluegrass	7	14	1.78 [122]	1.89 [164]
Poa infirma	early meadow- grass	7	7	1.17 [165]	1.13 [165]
Poa supina	supine bluegrass	7	7	0.66 [165]	0.64 [165]
Setaria viridis	green foxtail	9	9	0.40 [166]	0.40 [166]
Striga asiatica	red witchweed	12	12	0.6 [167]	0.47 [167]
Striga hermonthica	purple witchweed	10	20	1.48 [168]	0.96 [168]
Thlaspi arvensis	field pennycress	7	7	0.5 [169]	0.53 [169]

938

Table 2. Genomic information for 19 weed species produced without assistance by the

940 International Weed Genomics Consortium. Haploid (1n) genome size estimations are either

941 calculated through flow cytometry or k-mer estimation.

942

943 Figure 1. Process by which the International Weed Genomics Consortium operates.

944

945 Additional Files

46

- 946 Additional File 1 (.docx). Methods and results for visualizing and counting the metaphase
- 947 chromosomes of (1A): diploid *Lolium rigidum*; (1B): hexaploid *Avena fatua*; (1C): diploid
- 948 *Phalaris minor*; and (1D): tetraploid *Salsola tragus*.
- 949
- 950 Additional File 2 (.docx). List of completed and in-progress genome assemblies of weed species
- 951 pollinated by insects.

