


Genome size variation among common dandelion accessions informs their mode of reproduction and suggests the absence of sexual diploids in North America

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Abstract Apomixis is the ability of plants to produce asexual seeds, which are clones of the mother plant. The phenomenon of apomixis is tightly linked to ploidy, where diploids lack apomixis and reproduce sexually, while higher ploidy levels can exhibit apomixis. *Taraxacum* F.H.Wigg. species (dandelions) commonly exhibit apomixis; however, only limited studies have evaluated genome size variation of the iconic weedy dandelion, *Taraxacum officinale* F.H.Wigg. (common dandelion), particularly in North America. To evaluate the ploidy and reproductive biology of common dandelion, we created a global collection, with an emphasis on North America and determined genome size by evaluating seeds with flow cytometry. A total of 635 accessions were screened, and with the exception of two accessions from Germany and Austria, all were found to exclusively contain polyploid seed. The mode of reproduction of a sample of 96 of these accessions was observed by conducting emasculations. Our results indicate that the diploid, sexual cytotype of common dandelion may be absent in North America, while diploids were found in previously described areas of Central Europe. This suggests that the clonal lineages of common dandelion in North America may largely be

derivative from apomictic plants introduced from abroad. Furthermore, if all North American common dandelion is apomictic, it may be unreceptive to pollen, which may isolate it from other dandelion species and inform the potential for gene flow.

Keywords Apomixis · Common dandelion · Flow cytometry · Genome size · Ploidy · *Taraxacum officinale*

Introduction

The taxonomy of the *Taraxacum* F.H.Wigg. genus is complicated, with >40 sections comprising ~3000 species (Doll 1982; Kirschner and Štěpánek 1996). The genus originated in central Asia and is now spread worldwide. North American dandelions were introduced at the end of the Pleistocene across the Bering land bridge (van Soest 1958; Richards 1970) and were consciously introduced early in European settlement (Solbrig 1971). According to data published on the Flora of North America Web site and the Integrated Taxonomic Information System online database, there are 16 *Taraxacum* species that can be identified in North America, which belong to the following sections: sect. *Arctica* (*T. alaskanum* Rydb., *T. carneocoloratum* A.Nelson, *T. holmenianum* Sahlin, *T. hyparcticum* Dahlst., *T. phymatocarpum* J.Vahl, *T. scopulorum* Rydb.), sect. *Borealia* (*T. californicum* Munz & I.M.-Johnst., *T. ceratophorum* (Ledeb.) DC., *T. laurentianum* Fernald, *T. trigonolobum* Dahlst.), sect. *Erythrosperma* (*T. erythrospermum* Andr. ex Besser), Palustria (*T. palustre* (Lyons) Symons), sect. *Ruderalia* (*T. officinale* F.H.Wigg., *T. latilobum* DC.) and sect. *Spectabilia* (*T. lapponicum* Kihlm. ex Hand.-Mazz., *T. spectabile* Dahlst.) (Luc Brouillet 2006). Except *T. ceratophorum*, *T.*

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erythrospermum and *T. officinale*, which are widely distributed in North America, other species have limited, remote distributions (Luc Brouillet 2006; Integrated Taxonomic Information System online database 2017).

Apomictic *Taraxacum* exhibit meiotic diplospory, where megaspores are not reduced and develop into seeds that have the same genotype as the parent plant (van Dijk et al. 2009). Apomixis is an evolutionary dead end, due to a lack of recombination, which allows plants with new gene combinations to be generated and provides a means for deleterious mutations to be discarded. However, in the short term, apomixis allows strong genotypes to be fixed and potentially increases fitness by allowing the parent plant to contribute all of the genetic material of its offspring and produce full seed set without pollination.

In *Taraxacum*, polyploids are typically apomictic, while diploids are sexual (usually self-incompatible), as polyploidy is necessary to complement the lethality of mutations associated with apomixis loci (van Dijk 2003). Sexually reproducing, tetraploid dandelions, such as *Taraxacum* sect. *Piesis*, do co-occur with diploid cytotypes; however, this section has not been identified in North America (Kirschner and Štěpánek 1998; Závěský et al. 2005). In North America, *Taraxacum* includes apomictic polyploids, as well as rare, sexual diploids. Previous work has shown that triploid dandelions appear to produce seed exclusively through apomixis (van Baarlen et al. 2002). New clonal lineages arise when pollen from apomicts fertilizes sexual plants (Doll 1982). This allows apomixis genes to enter a new genetic background in order to generate adaptive clonal lineages and purge the genes of deleterious mutations, through crossing over during pollen meiosis.

Common dandelion (*Taraxacum officinale* F.H.Wigg.) is the most widely distributed *Taraxacum* in North America. It is considered native to Eurasia and brought to North America by European settlers, both intentionally and accidentally. In North America, common dandelion has come to be treated as a single species due to limitations in microspecies recognition, as well as lower levels of recognized diversity relative to Eurasia (Luc Brouillet 2006). In this study, we largely focused on North America and treated common dandelion as a single species belonging to *Taraxacum* sect. *Ruderalia*, based on phenotypes described by Luc Brouillet (2006).

Common dandelion is widely adapted to moderate disturbance and occurs commonly in mowed grass as well as in agriculture (e.g., pastures, hay fields, orchards, vineyards and strawberries), especially in reduced-tillage corn, soybean and wheat (Kapusta and Krausz 1993; Andersson and Milberg 1998; Stewart-Wade et al. 2002). Common dandelion reduces crop yields, delays drying of hay, is allelopathic and competes with fruit trees for pollinators

(Free 1968; Gyenes and Béres 2006). Both sexual and apomictic versions of common dandelion exist in nature. In Europe, apomictic populations are considered better adapted to marginal, stable environments where rapid population growth is important, whereas sexual diploids predominate in more variable environments where recombination allows them to adapt to fill specialized niches (van Dijk and van Damme 2000).

In spite of abundant time and opportunity for migration of diploid types, previous surveys have detected only the apomictic, triploid type of common dandelion in North America (Solbrig 1971; Lyman and Ellstrand 1984). However, these studies were limited in the number of accessions and geographic areas that were sampled, largely due to a lack of high-throughput screening methods. Understanding the potential reproductive pathways of North American common dandelion is critical, especially when exotic species are introduced. Given the imperative to produce sustainable biochemicals and bio-products, *Taraxacum* species may be cultivated on a large scale. One such species is *Taraxacum kok-saghyz*, which produces natural rubber in its roots (Bowers 1990; Mooibroek and Cornish 2000). Moreover, genetic engineering may be used to accelerate the domestication and ultimate adoption of future *Taraxacum* crops (Zhang et al. 2015). With this consideration, an understanding of how receptive weedy *Taraxacum* species (*T. officinale*) may be to pollen from cultivated varieties is essential. We believe the largest driver of this receptivity is the presence or absence of apomixis, which has not been fully characterized in North American *Taraxacum* populations. In order to enlarge the survey of North American common dandelion, flow cytometry was used to characterize the genome sizes of seed populations. Pools of seeds were selected for this study, as the composition of a diploid common dandelion flower head may contain a mix of polyploid and diploid progeny, where one category may predominate. By sampling pools of seeds derivative from a single flower head, a minority of diploid seeds could still be detected with a single sampling. We then went on to grow plants from seed accessions and characterize the reproductive biology of individual plants.

Materials and methods

Generation of global common dandelion collection

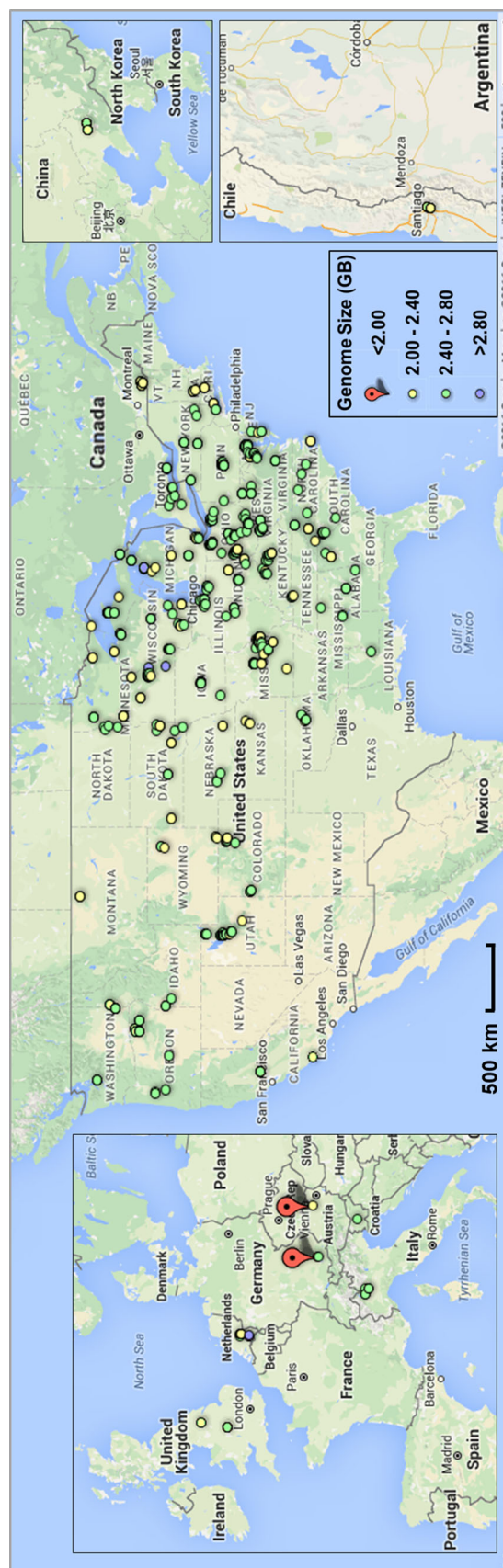
Requests for seed samples were sent to weed scientists and collaborators in all US states and Canadian provinces, as well as to colleagues working in Europe, Chile and China. Participants were instructed to collect all seeds from an individual flower head selected from four healthy plants

Fig. 1 Locations where common dandelion (*Taraxacum officinale*) samples were collected and their genome size category. GB, Gigabases. Accessions which contained diploid seed (genome sizes are smaller than 2.00 GB) are marked with a red flag. Accessions with genome sizes between 2.00 and 2.40 GB, 2.40 and 2.80 GB and greater than 2.80 GB were marked with yellow, green and purple dots, respectively

with common dandelion phenotype, separated by at least 10 m (Zhang et al. 2017). Seeds of all samples tested were of *T. officinale* morphology described by Luc Brouillet (2006), as were leaves and flowers of all those that were grown to maturity. In North America, the most widespread closely related species, *T. erythrospermum*, is less common and distinguished by its red seeds, while *T. ceratophorum*, which occurs in mountainous regions, is easily distinguished by flower and leaf morphology. While it is our expectation that *T. officinale* represented the vast majority of dandelions where our samples were collected, given the breadth of this survey and the number of different seed contributors, we cannot rule out the possibility of other species being present in this survey, depending on one's view of *Taraxacum* taxonomy. However, we do not believe this detracts from our ability to detect weedy, diploid common dandelion in North America. Seeds from the four plants were placed in separate envelopes labeled with location information. Among the accessions, 559 were collected from the USA, 16 were from Canada and 5 were from Chile. A total of 28 accessions were collected from Europe, including 9 from the Netherlands, 3 from Germany, 5 from Italy, 8 from Norway, 2 from Austria and 1 from Slovenia. Additionally, 5 accessions were collected from northeast China. A map showing the locations of all the accessions collected and scored is shown in Fig. 1. The coordinates and estimated genome sizes of each accession are also provided, in Online Resource 1.

Flow cytometry seed screening

Taraxacum seeds were subjected to genome size analysis. A total of 635 *Taraxacum* accessions were used for flow cytometry. Ten seeds from each *Taraxacum* accession were chopped in 1.4 ml of Galbraith's buffer amended with 1% (w/v) polyvinylpyrrolidone (PVP) m.w. 10 K (Galbraith et al. 1983). Seed fragments from radish (*Raphanus sativus* L. cv. Pink Beauty) were included as an internal standard, as its estimated genome size (1.05 Gigabases, GB (Kishishiba et al. 2014)) can be easily resolved from diploid or polyploid common dandelion and proved to be compatible with *Taraxacum* seeds in propidium iodide staining solutions (Galbraith et al. 2001; Doležel and Bartoš 2005; Sliwinska et al. 2005, 2009). The solution was then passed through a 30-micron nylon mesh filter and brought to a final volume of 1.5 ml, by adding suspensions of



propidium iodide and RNase to final concentrations of $50 \mu\text{g ml}^{-1}$ each. Samples were gently mixed and incubated in the dark for 20 min at 20°C . Samples were then run on a Partec Cyflow PA equipped with a green (532 nm) laser, at a speed of $0.3 \mu\text{l s}^{-1}$ and a lower limit of 0.73 until $100 \mu\text{l}$ had been sampled. Gains were adjusted such that the control exhibited a fluorescence value of 50.

Evaluation of reproductive biology

A sample of 96 accessions was selected for apomixis screening through emasculation. Individual plants from these accessions were grown from seed in Pro-Mix, under greenhouse conditions. Emasculations were conducted to detect apomixis using flower buds from stalks of at least 5 cm. Cuts were made roughly 0.5 cm above where bracts emerged using sterilized scissors. Three buds were sampled for each genotype tested. Buds were allowed to mature for three weeks after emasculation, before seed set was scored. Individual buds were bagged both before and after emasculation. Buds which produced filled, brown, germinable seeds after emasculation were counted as apomictic. Sexuality of select genotypes was tested by sealing buds in bags prior to anthesis. After flowers were fully open, a single open flower from a different genotype was used as a pollen donor, by gently rubbing the two flower heads together for approximately 10 s. The flowers of the pollen recipients were then resealed in bags and allowed to mature.

Data analysis

The histogram showing genome size distribution (Fig. 2) was plotted using Microsoft Excel 2013 (Version: 15.0.4823.1000). Data analysis of genome size distribution, as well as the boxplot and scatter plots, was generated using R (R Core Team 2013). The map of global common dandelion seed collection was generated using Google Map and Google Fusion Tables.

Results

Genome size and reproductive biology characterization of common dandelion

All common dandelions screened in North America proved to be DNA-polyploids, while DNA-diploids were detected as a minority in regions of Central Europe (Online Resource 1) (All polyploids and diploids identified in this study were considered DNA-polyploids and DNA-diploids, according to the convention established in Suda et al. (2006)). This was in line with previous studies showing the

presence of diploid common dandelions in Central and Western Europe (den Nijs et al. 1990; Menken et al. 1995; van Dijk 2003). All polyploid dandelions that were emasculated demonstrated apomixis, while all diploid dandelions reproduced sexually. These results suggest that North American common dandelion may be unreceptive to pollen, providing a degree of reproductive isolation. These data may inform frequencies of gene flow within common dandelion populations and between common dandelion and other dandelion species.

A histogram of the common dandelion genome sizes obtained by flow cytometry analysis of the global collection of 635 common dandelion accessions is shown in Fig. 2. The genome sizes of common dandelions sampled in this study ranged from 1.61 to 3.02 GB, with most of the accessions falling between 2.4 and 2.7 GB. Of these accessions, the majority (591) were from North America. Two diploid cytotypes with total genome sizes of 1.61 and 1.80 GB were detected in accessions from Munich, Germany and Durnstein, Austria, respectively. These diploid accessions contained seeds with both triploid and diploid cytotypes, suggesting these accessions originated from a diploid mother plant pollinated by both diploid and polyploid common dandelion. Diploid common dandelions within these accessions produced smaller, less full flowers than their apomictic counterparts (van Dijk et al. 2009). When grown and emasculated, diploid accessions demonstrated a lack of apomixis, while 96 selected polyploid common dandelion accessions invariably exhibited apomixis after emasculation. When selfed, the diploid common dandelions we detected did not produce seeds; however, viable seeds were produced when they were outcrossed.

The mean genome size of common dandelion considered to be polyploid was 2.503 GB (± 0.006), while the two diploid cytotypes had an average genome size of 1.707 GB. These results are consistent with previously reported values for these cytotypes (Bennett et al. 1982; Závěský et al. 2005). The mean polyploid genome sizes within Chile, China, Europe and North America were 2.321, 2.381, 2.538 and 2.501 GB, respectively. A boxplot of the genome sizes observed in each region is shown in Fig. 3. The mean coefficients for variance for the radish and common dandelion seed were 4.442 (± 0.575) and 3.796 (± 0.0433), respectively.

Discussion

A wide range of genome size was observed among apomictic common dandelion (2.08–3.02 GB). While many of these genomes are presumably unbalanced, the presence of apomixis allows unbalanced genomes to

Fig. 2 Histogram of the genome sizes observed in a global collection of 635 common dandelion (*Taraxacum officinale*) seed accessions

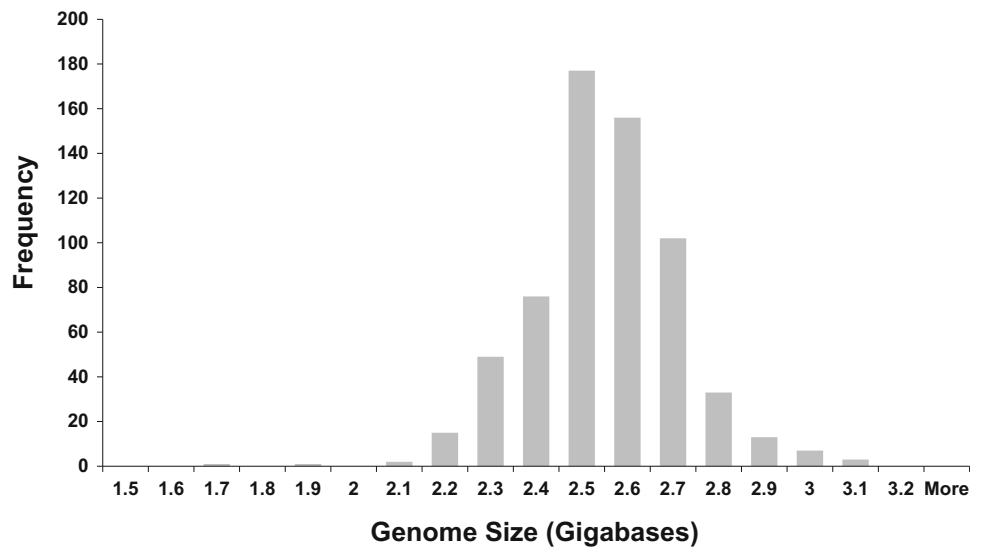
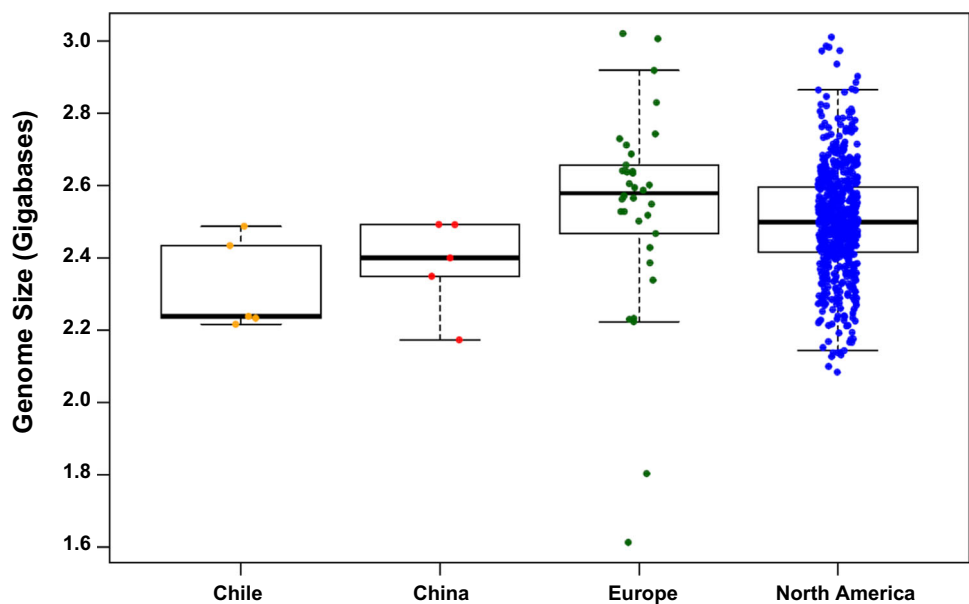


Fig. 3 Boxplot showing the common dandelion (*Taraxacum officinale*) genome size variation observed within the geographic regions sampled. Accessions sampled in Chile, China, Europe and North America are shown in yellow, red, green and blue dots, respectively. Two low outliers in Europe indicate the two diploid cytotypes



persist. This diversity may be due to unbalanced pollen contributions from polyploid common dandelion (van Baarlen et al. 2000; Mártonfióvá 2006). It is also possible that some of the diversity in genome sizes we observed is due to a history of hybridization, where plants with common dandelion phenotypes may have assimilated genomes of other species. Future work may be conducted to evaluate the genomic structure underlying the diversity we observed. Our results also suggest that there may be regional variations in genome size; however, more work, with larger sample sizes from outside North America, is needed to directly evaluate this.

Our results demonstrate an apparent absence of sexually reproducing common dandelion in North America. In such a case, all common dandelion diversity would be derived

from outside introductions of clonal lineages. However, while common dandelion in North America may be reproductively isolated on the maternal side, pollen produced by triploids still develops under normal reductional meiosis and can therefore contribute a range of balanced and unbalanced chromosome complements that may pollinate other diploid *Taraxacum* species. This type of hybridization between triploid common dandelion and native diploids has previously been observed (Shibaike et al. 2002; Brock 2004). This may provide a rare avenue for common dandelion in North America to obtain new genetic diversity and create new apomictic lineages. To determine if common dandelions are the result of such hybridizations with locally adapted diploids, chloroplast markers may be used to detect maternal ancestry (Shibaike

et al. 2002). In the absence of hybridization, new introductions of common dandelion from other regions, such as Europe, may provide a continued source of new common dandelion genotypes.

It is possible that our survey enriched for apomictic common dandelion, as they exhibit more weedy character and thrive in disturbed areas, while diploids may be in more isolated, niche environments. We expect that volunteers are much more likely to search for common dandelion in areas where apomictic polyploids are abundant. In order to detect potential rare diploid cytotypes, dandelions with only partial seed set may be targeted as this is a strong indicator of a lack of both apomixis and polyploidy.

It is our expectation that diploid common dandelion has been co-introduced into North America with an abundance of the triploid cytotype; however, it may be difficult for diploids to establish as they must compete with a profusion of polyploid pollen, which produces new polyploid progeny. Furthermore, given the relatively short evolutionary time since common dandelions were introduced into North America, the expected advantage of diploids being able to produce better adapted diploid and polyploid lines may not yet have been realized. Additionally, as new apomictic common dandelion is continually introduced from abroad, the capacity to reproduce sexually may lack an evolutionary incentive.

Conclusion

The genome size characterization of a global collection of 635 common dandelion accessions using flow cytometry suggests that all common dandelions screened in North America are apomictic polyploids, while sexual diploids were present in regions of Central Europe. This work may inform the potential and directionality of gene flow between and among *Taraxacum* species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Information on Electronic Supplementary Material

Online Resource 1. Common dandelion (*Taraxacum officinale*) collecting locations and estimated genome sizes.

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