



Genome size and ploidy levels of creeping phlox and related germplasm of mat-forming taxa from eastern and western North America



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ABSTRACT

The eastern North American creeping phlox (*Phlox subulata* L.) is a widely cultivated flowering ground-cover with a history of breeding and selection. Little is known about genome size variation and ploidy of *P. subulata* and related taxa. Mean holoploid (2C) and monoploid (1Cx) genome sizes and ploidy were analyzed with flow cytometry for a germplasm collection (n = 53) of 11 morphologically similar creeping phlox taxa from natural plant populations, cultivars and hybrids obtained from nursery sources, and the related *Microsteris gracilis*. Holoploid genome sizes of accessions from natural populations were more variable than cultivated taxa and ranged from 7.47 to 22.86 pg and corresponded to diploid (2n = 2x = 14) tetraploid (2n = 4x = 28), and hexaploid (2n = 6x = 42) levels, but most accessions were diploid and genome size ranged from 7.60 to 8.47 pg. Two tetraploid accessions were discovered, but hexaploids were limited to one population of *P. subulata*. Most accessions consisted of a single cytotype, but intrapopulation differences in holoploid genome size were found among *P. subulata* and *P. nivalis*. The monoploid genome size of *M. gracilis* differed significantly from all *Phlox*, supporting separation of the genera. All cultivar accessions were diploid with genome sizes similar to wild diploid *P. subulata*, however *Phlox* × *procumbens* had a mean genome size (8.73 pg) intermediate to parental taxa, *P. stolonifera* × *P. subulata*, supporting hybrid origin. Knowledge of cytotype variation in *Phlox* germplasm will be useful for plant breeders, systematists, and conservationists.

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1. Introduction

Phlox (Polemoniaceae) is an important genus of ornamental herbaceous plants previously targeted for germplasm development, characterization, and enhancement by the United States Department of Agriculture (USDA) National Plant Germplasm System (NPGS). *Phlox* species, cultivars, and interspecific hybrids are widely grown as versatile, flowering perennials that serve a variety of landscape functions (Bendtsen, 2009; Fuchs, 1994; Locklear, 2011). Among cultivated *Phlox* taxa, the “creeping phloxes” are a morphologically distinct group of evergreen subshrubs grown for their luxuriant, mat-forming growth habit, and “carpet of color” floral displays (Foley, 1972). As many as 80 cultivars are attributed to *Phlox subulata*; however, the breeding history of these

selections is poorly documented, and interspecific hybridization has likely been involved. (Bendtsen, 2009; Fuchs, 1994; Locklear, 2011; Wherry, 1955). The role of polyploidy in cultivar development is not known, and in general, little is known about ploidy or genome size in species or cultivars. Such information is an important component of germplasm characterization that could guide plant breeders and also provide insight about the history of hybridization among various taxa.

Polyploidy is an important factor in plant breeding because it can influence reproductive compatibility, fertility, and expression of phenotypic traits (Ranney, 2006). The manipulation of ploidy has been an important tool in the development of many ornamental cultivars (Ranney, 2006) and artificial polyploids have been induced in *Phlox drummondii* (Vyas et al., 2007), *Phlox paniculata* (Matiska and Vejsadová, 2010) and *P. subulata* (Zhang et al., 2008), although it is unclear if any of these polyploids have been used as germplasm resources. Polyploidy was considered rare in the genus *Phlox*, but recent studies have indicated that it is more prevalent than

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previously reported, and that it may be an important mechanism for genetic diversification, reproductive isolation, and exploitation of new ecological niches. (Fehlberg and Ferguson, 2012; Flory, 1931, 1934; Levin, 1983; Meyer, 1944; Soltis et al., 2009; Theodoridis et al., 2013; Worcester et al., 2012; Wright, 2014). Information about genome size and ploidy is still lacking for most *Phlox* species, and there are even fewer reports of genome size for *Phlox* cultivars (Zale and Jourdan, 2015); such information is essential for germplasm characterization and potential use in breeding, as well as for more fundamental studies of taxonomic relationship and speciation.

Phlox is a phenotypically and ecologically diverse genus of approximately 65 species native to temperate regions of North America, with one outlying species in Russia (Ferguson et al., 1999; Locklear, 2011; Wherry, 1955). Within the United States there are two centers of diversity: one in the eastern region of the continent that comprises 20–23 species, and the other in the western region that includes the remaining species (Wherry, 1955). The majority of cultivated *Phlox* come from the eastern U.S. species (Locklear, 2011). Wherry (1955) conducted the most comprehensive taxonomic study of the genus and organized it into three sections and 16 subsections on the basis of morphology and geographic distribution, but admitted that his classification was “rather artificial”, and that certain taxa “bridged key gaps” between subsections. In Wherry’s classification, the eastern species are grouped into sections *Annuae* and *Phlox* and further assigned to seven subsections; the western species were placed in section *Occidentales*. Among the eastern group, subsection *Subulatae* includes the creeping or moss phloxes that consist of four phenotypically distinct species and up to eight subspecies. These taxa are distinguished from other eastern species in being suffrutescent, caespitose or pulvinate, sclerophyllous shrubs that are superficially similar to many western taxa (Ferguson et al., 1999; Ferguson and Jansen, 2002; Wherry, 1929, 1955). Initially, Wherry split these eastern taxa among subsections *Speciosae* and *Subulatae* on the basis of differences in style length. Recent molecular phylogenetic analysis revealed that all eastern creeping phlox species formed a well-supported monophyletic group, regardless of style length variation, and there was strong support for placing subsection *Subulatae* in section *Occidentales* instead of section *Phlox*, as it was nested among a clade containing morphologically similar western taxa (Ferguson and Jansen, 2002). Although there is support for a close evolutionary relationship of eastern and western mat-forming taxa, relatively few western taxa were used in the analysis and the relationship needs further study and resolution. Genome size studies could provide an additional means of examining the relationships of these taxa.

Few species in subsection *Subulatae* and related western taxa have been thoroughly examined for chromosome counts and general ploidy levels (Flory, 1934; Meyer, 1944), and as indicated by Ferguson et al. (1999) “. . . more detailed examination of phylogenetic relationships with relation to chromosome numbers is warranted.” Early studies of chromosomes of two *P. subulata* cultivars showed they were diploid ($2n = 14$), and two wild collections labeled as “*P. subulata brittonii*” were also diploid (Flory, 1931, 1934). The most comprehensive karyological studies of *P. subulata* to date, found both diploid and tetraploid forms of the species; specimens labeled as *P. nivalis* × *P. subulata* hybrids were both diploid and tetraploid (Meyer, 1944). However, there was no collection locality information and the cultivars were not identified, so the data could not be used to delineate ploidy patterns of wild populations or cultivated taxa. A later study reported the chromosome number for a collection of *P. subulata* from Coshocton County, Ohio as “14 + 28”, suggesting a mixed ploidy population, but the significance of this find was not addressed further (Smith and Levin, 1967). A few studies suggest that ploidy variation among western

species may be greater than among eastern species (Eater, 1967; Flory, 1937, 1948; Strakosh, 2004; Wright, 2014). Most notably, a study of the *P. amabilis*-*P. woodhousei* complex revealed extensive variation in ploidy levels (cytotypes), ranging from diploid to hexaploid, with a serial increase in genome size (Fehlberg and Ferguson, 2012). A similar result was found among taxa in the *P. nana* complex (Wright, 2014). However, cytotype variation was also found for the eastern species *P. pilosa* of subsection *Divaricatae* suggesting that cytotype variation may be widespread throughout the genus (Worcester et al., 2012). It is evident that ploidy can be variable among western mat-forming taxa and it is possible that the same degree of variation could be found among similar taxa in subsection *Subulatae*.

Evergreen, creeping habit is not restricted to taxa in subsection *Subulatae*. Two species that comprise subsection *Stoloniferae*, *P. stolonifera* and *P. adsurgens*, also exhibit a caespitose habit, but are differentiated from other creeping phlox by their ovate to oblong-elliptic leaves and a larger inflorescence with more flowers borne on a long pedicel (Locklear, 2011; Wherry, 1955). These species exhibit vicariant distributions; *P. stolonifera* is endemic to mountainous provinces of the eastern U.S., and *P. adsurgens* is endemic to the U.S. Pacific Northwest (Wherry, 1955). Molecular and karyotypic evidence indicated that *P. stolonifera* is basal to the rest of the genus, but the phylogenetic placement of this species remains unclear (Ferguson et al., 1999). Despite divergent morphological characteristics and phylogenetic placement, both taxa in subsection *Stoloniferae* have been successfully hybridized with taxa from subsection *Subulatae*. Two artificial hybrids have been reported from plants in cultivation: *P. stolonifera* × *P. subulata*, known as *Phlox* × *procumbens*, and *P. adsurgens* × *P. nivalis*, known as *Phlox* × *oliveri* (Locklear, 2011; Wherry, 1935). Flory (1934) studied the meiosis of *P. × procumbens* and discovered several irregularities that supported hybrid origin. Due to different ecological requirements and geographic distributions, neither of these hybrids has been found in natural settings.

The objectives of this study were to determine genome sizes and ploidy levels of creeping phlox taxa in *Phlox* subsections *Subulatae* and *Stoloniferae*, and to compare these to some species from the western U.S. The taxa sampled also included cultivars and inter-specific hybrids from subsection *Subulatae*.

2. Materials and methods

2.1. *Phlox* collection

Living plants were obtained from nursery sources and from collection sites in the east-central United States that were visited from 2010 to 2013. Taxa collected from natural plant populations were identified using the taxonomic keys of Locklear (2011) and Wherry (1955), information from phylogenetic analyses of Ferguson et al. (1999) and Ferguson and Jansen (2002), and comparison with herbarium specimens from regional herbaria. Cultivars and hybrids were obtained from nursery sources and identified using a variety of sources (Bendtsen, 2009; Fuchs, 1994). Herbarium vouchers are maintained at the Ornamental Plant Germplasm Center (OPGC), Columbus, OH.

2.2. Plant cultivation

Plants were grown in a greenhouse as described by Zale and Jourdan (2015). Samples from these plants were used for chromosome and flow cytometry analysis.

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