

CHROMOSOME NUMBERS OF NORTH AMERICAN *LATHYRUS* (FABACEAE)

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ABSTRACT

Chromosome counts are reported for 18 populations of eight perennial *Lathyrus* species endemic to North America. Included are first counts of $2n=14$ for *L. holochlorus* (Piper) C. Hitchc., *L. delnorticus* C. Hitchc., *L. glandulosus* Broich, *L. jepsonii* E. Greene subsp. *jepsonii* and *L. vestitus* Nutt. in Torrey & A. Gray subsp. *vestitus*, and $2n=28$ for *L. nevadensis* S. Watson subsp. *nevadensis*. Chromosome counts of $2n=14$ for *L. jepsonii* subsp. *californicus* (S. Watson) C. Hitchc., *L. vestitus* subsp. *bolanderi* (S. Watson) C. Hitchc., *L. polyphyllus* Nutt. in Torrey & A. Gray and *L. sulphureus* Brewer ex A. Gray agree with those reported previously. Karyotypes of diploid species are symmetrical and similar to one another. Among the species studied here there does not appear to be the reduction in chromosome size and DNA amount reported in the literature for annual, autogamous Mediterranean *Lathyrus* species.

Lathyrus L. is a genus of approximately 150 species of herbaceous perennial and annual papilionoid legumes (Fabaceae: Faboideae: Viciaeae). The genus is distributed primarily in temperate Europe, Asia, North America, and South America, and in North Africa (Senn 1938; Kupicha 1981, 1983). There are about 26 species of *Lathyrus* endemic to North America (Hitchcock 1952; Welsh 1965; Barneby and Reveal 1971; Broich 1983, 1986, 1987; Nelson and Nelson 1983; Welsh et al. 1987); chromosome numbers have been reported for 15 of these species (Senn 1938; Hitchcock 1952; Ledingham 1957; Brunsberg 1965; Raven et al. 1965; Taylor and Mulligan 1968; Löve and Löve 1982; Ward 1983).

The purpose of this paper is to report new observations of chromosome number and morphology of species of *Lathyrus* endemic to North America and to place these observations within the context of the genus world-wide.

MATERIALS AND METHODS

Seeds of native *Lathyrus* were collected in July of 1979, 1980, and 1981. In addition to the author's collections, seeds of *L. jepsonii* E. Greene subsp. *jepsonii* were obtained from W. Roderick (Tilden Park Botanical Garden, Berkeley, CA), of *L. vestitus* Nutt. in Torrey & A. Gray and *L. laetiflorus* E. Greene (= *L. vestitus* subsp. *vestitus* sensu Broich, 1987) were obtained from Mary Allcott (Santa Barbara Botanic Garden, Santa Barbara, CA) and of *L. vestitus* from Mon-

terey County, CA, were obtained from Dr. J. R. Griffin (Hastings Natural History Reservation, Carmel Valley, CA).

Seeds were scarified with a razor blade and stored in rolls of damp germination paper (Dillard Paper Co., Doraville, GA) in a refrigerator at ca. 5°C for 2 months. Five to six rolls were then placed vertically in a glass jar containing 100 ml of tap water, covered with a clear plastic bag and placed in a growth chamber on a cycle of 18 hours light at 22°C and 6 hours darkness at 18°C. After germination, seedlings were transplanted to the greenhouse into a soil mixture of equal parts of sand, peat, and soil.

The number and morphology of mitotic chromosomes were studied by examining root tip squashes. Root tips were pretreated with distilled water saturated with para-dichlorol-benzene at 10–15°C for 4 hours, fixed in 95% ethanol:glacial acetic acid (3:1; v:v), hydrolyzed in 1 N HCl for 20 minutes at 60°C, stained in Feulgen (Darlington and La Cour 1975) and stored in 70% ethanol in a refrigerator (ca. 5°C). Stained root tips were squashed in 45% acetic acid and examined and photographed on a Zeiss phase-contrast microscope; slides were not made permanent.

Voucher specimens, deposited at Oregon State University Herbarium (OSC), were made from two sources: specimens of plants taken from populations where seeds were later collected (field vouchers), and specimens of the plants from which root tips were taken (greenhouse vouchers). The species of *Lathyrus* studied here did not flower under greenhouse conditions, therefore the greenhouse voucher specimens are of vegetative stems only.

RESULTS

Table 1 presents a summary of new chromosome counts for Pacific Coast *Lathyrus*. First counts of $2n=14$ were determined for *L. glandulosus*, *L. holochlorus*, *L. delnorticus*, *L. jepsonii* subsp. *jepsonii* and *L. vestitus* subsp. *vestitus*, and a count of $2n=28$ for *L. nevadensis* subsp. *nevadensis*. Additional counts of $2n=14$ for *L. jepsonii* subsp. *californicus*, *L. polyphyllus*, *L. sulphureus*, *L. vestitus* subsp. *bolanderi* agree with the reports of Hitchcock (1952).

Karyotypes of all species examined are symmetrical and fall into classes 1A and 1B described by Stebbins (1971). Chromosome complements of these species are similar to one another; there is less than 25% difference in total haploid chromosome length among all diploid species examined. Chromosomes within a species are also similar to one another; the ratio of longest to shortest chromosome within a given species ranged from 1.4 to 1.7. The genome of each diploid species consists of 3–4 metacentric chromosomes decreasing in length from 7.1 to 5.5 micrometers and 4–3 submetacentric chromosomes also decreasing in length from ca. 7.0 to 5.0 micrometers.

TABLE 1. NEW CHROMOSOME COUNTS OF PACIFIC COAST SPECIES OF *LATHYRUS*. An asterisk indicates first count(s) for that taxon.

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- **L. delnorticus* C. Hitchc. $2n=14$. CA, Del Norte Co., Panther Flat Campground, Six Rivers National Forest, T16N R3E sect. 22, *Broich* 642 (OSC); along French Hills Rd, 0.5 km S of jctn with Hwy 199, T17N R1E sects. 24–25, *Broich* 654 (OSC).
- **L. holochlorus* (Piper) C. Hitchc. $2n=14$. OR, Benton Co., along Oak Creek Rd ca. 0.4 km S of entrance to McDonald State Forest, T11S R5W sect. 19, *Broich* 1298 (OSC); Linn Co., along Hwy 99E opposite Linn-Benton Community College, T11S R4W sect. 36, *Broich* 630 (OSC).
- **L. glandulosus* Broich. $2n=14$. CA, Humboldt Co., 0.6 km E of the Freshwater-Kneeland Rd on rd to Maple Cr., *Broich* 772 (OSC); ca. 6.4 km S of the Kneeland School on rd to Bridgeville, *Broich* 777 (OSC).
- **L. jepsonii* E. Greene subsp. *jepsonii*. $2n=14$. CA, Contra Costa Co., Brown's Island near Pittsburg. Plants grown in greenhouse from seed provided by W. Roderick, Tilden Park Bot. Gard., Berkeley, CA, *Broich* 1278 (OSC).
- L. jepsonii* E. Greene subsp. *californicus* (S. Watson) C. Hitchc. $2n=14$. CA, Trinity Co., 1.3 km E of Dinsmore's on Hwy 36, T30N R5E sect. 3, *Broich* 1166 (OSC).
- **L. nevadensis* subsp. *nevadensis*. $2n=28$. OR, Benton Co., ca. 0.2 km S of entrance to McDonald State Forest, T121S R5W sect. 19, *Broich* 608 (OSC).
- L. polyphyllus* Nutt. in Torrey & A. Gray. $2n=14$. CA, Siskiyou Co., 3.9 km N of Happy Camp on rd to Takilma, Oregon, *Broich* 1182 (OSC). OR, Linn Co., along Peoria Rd, T12S R4W sect. 8, *Broich* 615 (OSC). Benton Co., McDonald State Forest, ca. 300 m N of the Oak Creek Entrance, T11S R5W sect. 19, *Broich* 1103 (OSC); along Peterson Rd, T12S R6W sect. 35, *Broich* 603 (OSC).
- L. sulphureus* Brewer ex A. Gray. $2n=14$. OR, Josephine Co., 0.8 km S of Waldo on FS rd 40S03, T40S R8W sect. 28, *Broich* 1131 (OSC).
- **L. vestitus* Nutt. in Torrey & A. Gray subsp. *vestitus*. $2n=14$. CA, Monterey Co., S slope of Junipero Serra Peak, Los Padres National Forest, T21S R5E sect. 4, plants grown in greenhouse from seed provided by J. R. Griffin, Hastings Natural History Reservation, Carmel Valley, *Broich* 1277 (OSC). Santa Barbara Co., plants grown in greenhouse from seed provided by Mary Allcott, Santa Barbara Botanic Garden, *Broich* 1267 (OSC). Ventura Co., ca. 64 km S of Ventucopa on Hwy 33, Los Padres National Forest, *Broich* 808 (OSC).
- L. vestitus* subsp. *bolanderi* (S. Watson) C. Hitchc. $2n=14$. CA, Del Norte Co., Panther Flat Campground, Six Rivers National Forest, T17N R3E sect. 22, *Broich* 643 (OSC).
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Chromosomes in the tetraploid *L. nevadensis* were also metacentric to submetacentric and of approximately the same length as those of diploid species.

On average, 5–10 good metaphase spreads were observed per root tip prepared, but in most cases only 1–2 photographs per plant were taken for measurement. Differences in degree of contraction were observed on slides and also among the photographs taken. Given the small sample size for each species and the karyotype similarity among species studied, interspecific differences could not be detected over the possible sources of error involved in karyotype measurements (Bentzer et al. 1971).

TABLE 2. A CATALOGUE OF CHROMOSOME COUNTS FOR SPECIES OF *LATHYRUS* ENDEMIC TO NORTH AMERICA. (* indicates reported herein; see Table 1.)

Species	<i>n</i>	<i>2n</i>	Previous report(s)
<i>L. biflorus</i> Nelson & Nelson	—	unknown	—
<i>L. bijugatus</i> White	—	unknown	—
<i>L. brachycalyx</i> Rydb.			
var. <i>brachycalyx</i>	—	14	Hitchcock 1952
var. <i>zionis</i> (C. Hitchc.) Welsh	—	14	Hitchcock 1952 [as <i>L. zionis</i> C. Hitchc.]
<i>L. delnorticus</i> C. Hitchc.	—	14*	—
<i>L. eucosmus</i> Butters & St. John	—	14	Hitchcock 1952
<i>L. glandulosus</i> Broich	—	14*	—
<i>L. graminifolius</i> (S. Watson) T. White	7	—	Hitchcock 1952; Ward 1983
<i>L. hitchcockianus</i> Barneby & Reveal	—	unknown	—
<i>L. holochlorus</i> (Piper) C. Hitchc.	—	14*	—
<i>L. jepsonii</i> E. Greene	—	14*	—
subsp. <i>jepsonii</i>	—	14*	—
subsp. <i>californicus</i> (S. Watson) C. Hitchc.	7	14*	Hitchcock 1952
<i>L. lanszwertii</i> Kellogg			
subsp. <i>lanszwertii</i>	14	14, 28	Hitchcock 1952
subsp. <i>aridus</i> (Piper) R. Bradshaw	7	14	Hitchcock 1952
var. <i>arizonicus</i> (Britton) Welsh	14	28	Hitchcock 1952 [as <i>L. arizonicus</i>]
var. <i>laetivirens</i> (E. Greene) Welsh	—	unknown	—
<i>L. littoralis</i> (Nutt.) Endl.	—	28	Taylor and Mulligan 1968
<i>L. longipes</i> T. White	—	unknown	—
<i>L. nevadensis</i> S. Watson			
subsp. <i>nevadensis</i>	—	28*	—
subsp. <i>cusickii</i> (S. Watson) C. Hitchc.	—	unknown	—
subsp. <i>lanceolatus</i> (Howell) C. Hitchc.	14	28	Hitchcock 1952

TABLE 2. CONTINUED.

Species	<i>n</i>	<i>2n</i>	Previous report(s)
<i>L. ochroleucus</i> Hook.	—	14	Senn 1938; Ledingham 1957; Löve and Löve 1982
<i>L. parviflorus</i> S. Watson	—	unknown	—
<i>L. pauciflorus</i> Fern.			
subsp. <i>pauciflorus</i>		unknown	—
subsp. <i>brownii</i> (Eastw.) Piper		unknown	—
<i>L. polymorphus</i> Nutt.		unknown	—
<i>L. polyphyllus</i> Nutt. in Torrey & A. Gray	—	14*	Hitchcock 1952
<i>L. rigidus</i> T. White	—	14	Hitchcock 1952
<i>L. splendens</i> Kellogg	7	14	Hitchcock 1952
<i>L. sulphureus</i> Brewer ex A. Gray	7	14*	Hitchcock 1952
<i>L. torreyi</i> A. Gray	7	—	Hitchcock 1952
<i>L. tracyi</i> R. Bradshaw	7	—	Hitchcock 1952
<i>L. venosus</i> Muhl. ex Willd.	14	28	Senn 1938; Ledingham 1957; Löve and Löve 1982
<i>L. vestitus</i> Nutt. in Torrey & A. Gray			
subsp. <i>vestitus</i>	—	14*	—
subsp. <i>laetiflorus</i> (E. Greene) Broich	—	14	Brunsberg 1965 [as <i>L. laetiflorus</i> E. Greene]
subsp. <i>alefeldii</i> (T. White) Broich	7	—	Hitchcock 1952 [as <i>L. laetiflorus</i> subsp. <i>alefeldii</i> (T. White) C. Hitchc.]
subsp. <i>bolanderi</i> (S. Watson) C. Hitchc.	7	14*	Hitchcock 1952
subsp. <i>laevicarpus</i> Broich	7	—	Raven et al. 1965 [as <i>L. laetiflorus</i> E. Greene]

DISCUSSION

Lathyrus is widespread in temperate regions of both the Old and New World. Bassler (1973) and Raven and Axelrod (1978) have suggested that the genus originated in the Arcto-Tertiary geoflora of the Eocene. *Lathyrus* now consists of approximately 75% perennials and 25% annuals organized into 13 sections (Kupicha 1983). Six sections consist exclusively of perennials, six sections of annuals and one section includes both perennials and annuals. All species endemic to North America are perennials and included in the section *Orobus* (L.) Godron in Gren. & Godron, which contains about one-third of all *Lathyrus* species.

Lathyrus L. is predominantly diploid at $2n=2x=14$. Kupicha (1977), in a summary table of counts for 56 species, reports five species which deviate from this number; Fedorov (1969) listed five polyploid species and two aneuploids (one $2n=12$; one $2n=16$) of 61 species reported. The Fedorov list, however, does not include counts reported by Hitchcock (1952). When information from Hitchcock (1952) and more recent compilations (Moore 1973; Goldblatt 1981, 1984, 1985) are taken into account, a total of seven polyploid taxa have been reported in *Lathyrus*. All polyploid taxa are perennial and belong to the section *Orobus* except *L. patensis* L. ($2n=14, 28, 42$) which has been placed in sect. *Pratensis* Bassler (Kupicha 1983).

With the new determinations reported here, a sample of chromosome numbers is now known for 18 of the 26 *Lathyrus* species endemic to North America (Table 2). North America appears to be a center for polyploidy in *Lathyrus*: four of the seven known polyploid species (*L. venosus* Muhl., $2n=28$; *L. nevadensis* S. Watson, $2n=28$; *L. littoralis* (Nutt. ex Torrey & A. Gray) Endl., $2n=28$; *L. lanzwertii* Kellogg, $2n=14, 28$) are endemic to the continent; two of the remaining three (*L. japonicus* Willd., $2n=14, 28$; *L. palustris* L., $2n=42$) have circumboreal distributions and are native to North America. The complete extent and significance of polyploidy in North American *Lathyrus* have yet to be studied in detail.

Variation in the amount of genome DNA among *Lathyrus* species has also been studied (Rees and Hazarika 1969; Narayan 1982). Annual, autogamous species, which have evolved in the Mediterranean region, exhibit a threefold decrease in chromosome size correlated to a fourfold decrease in the amount of nuclear DNA per diploid nucleus. In contrast, all western North American species of *Lathyrus* are perennial. Of those occurring along the Pacific Coast, *L. vestitus* subsp. *bolanderi*, *L. holochlorus*, and *L. polyphyllus* have been found to be self-incompatible (Broich 1983). *L. vestitus* is reported as having the greatest amount of nuclear DNA of the 21 species studied by Narayan (1982), and if chromosome size can be

taken to indicate, approximately, nuclear DNA amounts within a genome, the other species studied here have similar high amounts of DNA in comparison to the annual species of the Mediterranean Region. New chromosome observations reported here, therefore, corroborate the correlation between reduced DNA amounts and the evolution of an annual habit reported for *Lathyrus* (Rees and Hazarika 1969) and for higher plants in general (Price 1976).

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