American Journal of Botany 91(6): 889–898. 2004.

Diploid and polyploid cytotype distribution in *Melampodium cinereum* and *M. leucanthum* (Asteraceae, Heliantheae)[1]

Tod F. Stuessy,[2,4] Hanna Weiss-Schneeweiss,[2] and David J. Keil[3]

[2]Department of Higher Plant Systematics and Evolution, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria; and
[3]Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407 USA

Previous chromosomal studies within *Melampodium* (Asteraceae, Heliantheae) of Mexico and Central America have documented chromosome numbers $n = 9$, 10, 11, 12, 18, 20, 23, 25 ± 1, 27, 30, and 33. Some species also have been shown to exhibit infra- and interpopulational polyploidy. The presence of cytotype mixtures is especially pronounced in the white-rayed complex, which occurs in the southwestern United States and adjacent Mexico. This group includes *M. cinereum* ($n = 10$ and 20), *M. leucanthum* ($n = 10$ and 20), and *M. argophyllum* ($n = 30$). Cytotype distribution has been newly analyzed in 415 plants from 152 populations and added to existing data from 185 plants from 113 populations, yielding information from a total of 600 individuals from 265 populations. Within *M. cinereum* and *M. leucanthum* are parapatric distributions of cytotypes, with tetraploids centered in the eastern and diploids in the western portions of their ranges. Tetraploids are most likely of autopolyploid origin, forming recurrently, with adaptations that allow colonization and establishment in new ecological regions. Contact zones are relatively narrow and only two triploid individuals have been detected. The tetraploid cytotypes probably extended eastward into central and southern Texas to the natural barriers at the edge of the Edward's Plateau in *M. leucanthum* and the low sandy plains in *M. cinereum*. The hexaploid *M. argophyllum* is interpreted as a relict surviving in the low mountains of northern Mexico; it may be an allopolyploid of hybrid origin between ancestors of the evolutionary lines that eventually yielded *M. cinereum* and *M. leucanthum*.

Key words: Asteraceae; autopolyploidy; chromosome numbers; contact zones; cytotypes; Heliantheae; *Melampodium*.

Although known for decades, the occurrence of polyploid races within plant species continues to be of interest to plant systematists and evolutionists. The occurrence of polyploidy among angiosperm species has been estimated to be 30% (Stebbins, 1971) to 80% (Goldblatt, 1980; Leitch and Bennett, 1997). Some studies (see Levin, 2002, for review) have suggested that polyploidy has played a much more important role in plant evolution than believed previously (e.g., Stebbins, 1971) and that autopolyploids may originate recurrently within diploid taxa (Soltis and Soltis, 1993, 1999, 2000; Wendel, 2000; Ramsey and Schemske, 2002). The significant questions regarding polyploidy relate to mechanisms of their origin, establishment relative to diploid progenitors, and coexistence of the chromosomal races, especially in contact zones (Petit et al., 1999). Mechanisms of autopolyploid origin have been studied in detail (Jackson and Casey, 1982; Jackson and Hauber, 1982; Felber, 1991). Establishment of autopolyploids relative to diploid progenitors has also been examined (Levin, 1975; Felber, 1991; Bever and Felber, 1992; Rodriguez, 1996) with examples of distributions of infraspecific polyploid races (e.g., Kay, 1969; Mooring, 1980; Chmielewski and Semple, 1983; Nicholson, 1983; Soejima, 1992; Pak et al., 1995; Husband and Schemske, 1998; McArthur and Sanderson, 1999).

Melampodium (Asteraceae, Heliantheae) contains 39 species distributed throughout Mexico and Central America (Stuessy, 1972; Turner, 1988, 1993). Previous studies in the genus have revealed variation in chromosome numbers from the infraspecific to the infrageneric levels (Turner and King, 1962; Turner and Flyr, 1966; Stuessy, 1971b; Solbrig et al., 1972; Keil and Pinkava, 1976; Pinkava and Keil, 1977; Powell and Powell, 1977, 1978; Schaack, 1982; Strother, 1983; Ward, 1983). At the broadest level, haploid numbers of $n = 9$, 10, 11, 12, 18, 20, 23, 25 ± 1, 27, 30, and 33 have led to changes in classification and interpretation of the phylogeny in the group (Stuessy, 1971b). At the specific level, chromosomal differences between taxa have been useful for interpreting species limits, such as $n = 9$ in *M. microcephalum* vs. $n = 18$ and 27 in the related *M. paniculatum* (Stuessy, 1971b, 1972; Stuessy and Brunken, 1979). Chromosomal information, in consort with geographical data, have also been used to interpret isolating mechanisms and their roles in speciation within the genus (Sundberg and Stuessy, 1990).

At least four species of *Melampodium* possess two cytotypes: *M. cinereum* ($n = 10$ and 20), *M. dicoelocarpum* ($n = 12$ and 23), *M. leucanthum* ($n = 10$ and 20), and *M. paniculatum* ($n = 18$ and 27) (Stuessy, 1971b). The most well-studied example of infraspecific chromosomal variation occurs within the white-rayed complex of the genus (Stuessy, 1971b), including *M. cinereum* and *M. leucanthum*, distributed in the southwestern USA and adjacent northeastern Mexico. Viewed as one of the most advanced evolutionary lineages within the genus (Stuessy, 1979), the white-rayed complex is likely to have been influenced by relatively recent environmental changes, especially during the Pleistocene. We selected these two species to examine polyploid formation and their co-existence with diploids in more detail because they contain polyploid cytological races, most likely of autopolyploid origin (Stuessy, 1971a; Sundberg and Stuessy, 1990). Additionally, we examined *M. argophyllum*, once regarded as a variety of *M. leucanthum* (Stuessy, 1969).

[1] Manuscript received 17 July 2003; revision accepted 22 January 2004.

We thank Sigma Xi Grant-In-Aid of Research (to T. F. S.) in support of some of the fieldwork, the Graduate School of The Ohio State University for major support of collecting activities for many of the cited populations, and Lara Menon for technical assistance. Costs for manuscript preparation were supported by grant number P-15225-BIO (to T. F. S.) from the Austrian National Science Foundation (FWF).

[4] E-mail: tod.stuessy@univie.ac.at.

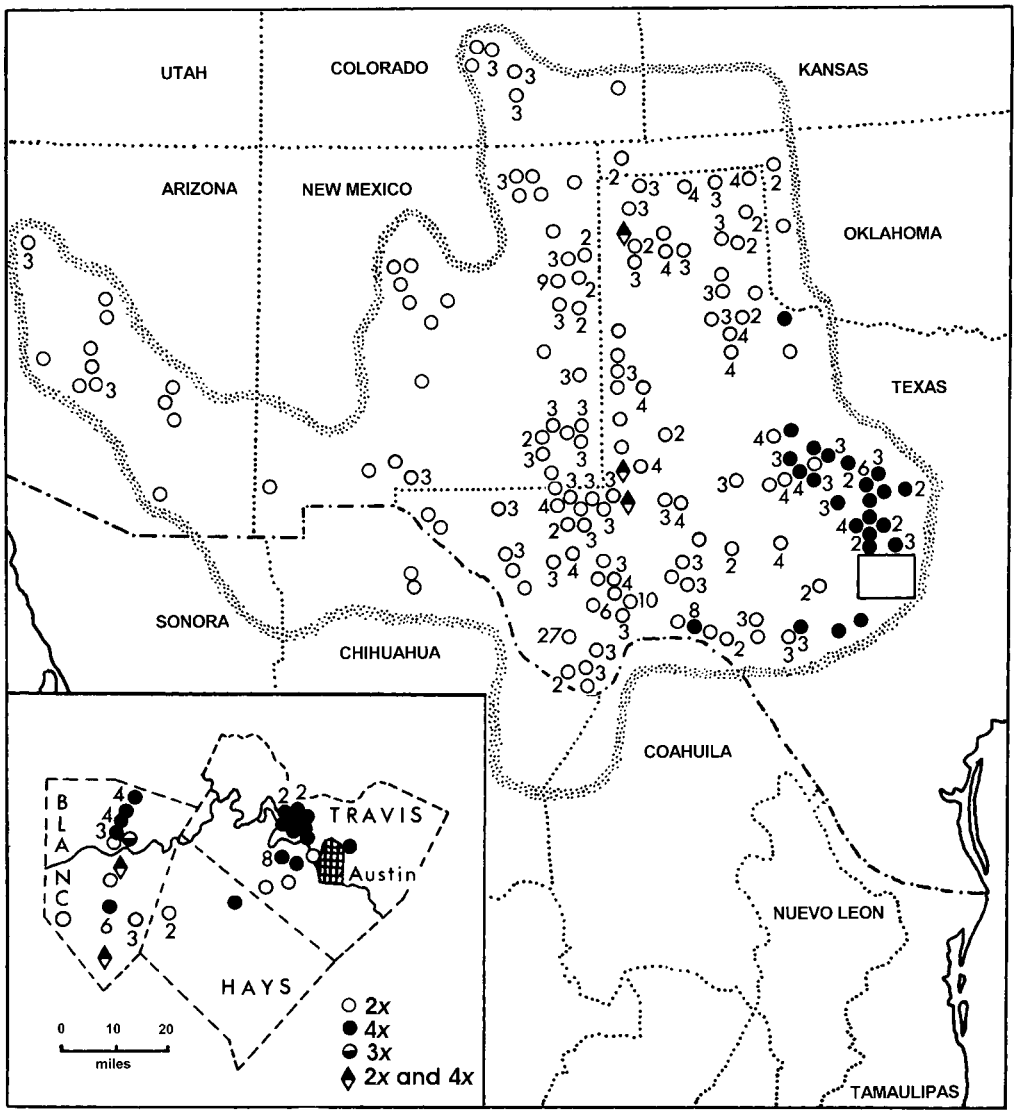

Fig. 1. Distribution in the southwestern United States and adjacent Mexico of chromosome counts in populations of *Melampodium leucanthum*. Numbers indicate individuals counted in each population (if more than one). Data in part from Stuessy (1971a, b), Solbrig et al. (1972), Keil and Pinkava (1976), Pinkava and Keil (1977), Powell and Powell (1977, 1978), Schaack (1982), Strother (1983), and Ward (1983). Stippled boundary indicates generalized distribution of the species. Inset map shows detailed populational distributions in Blanco, Hays, and Travis counties, Texas. Conversion: 1 mi = 1.6 km.

The purposes of this paper, therefore, are to: (1) document in detail the existence of diploid and polyploid cytological races within *Melampodium cinereum* and *M. leucanthum*; (2) characterize their contact zones; (3) discuss mechanisms leading to polyploid formation and establishment within the range of the diploids; and (4) examine the evolutionary and biogeographic implications of distributions of the chromosomal races.

MATERIALS AND METHODS

Flower buds of *Melampodium cinereum*, *M. leucanthum*, and *M. argophyllum* were collected in the field and fixed in modified Carnoy's solution (4 chloroform : 3 absolute ethanol : 1 glacial acetic acid), transferred to 70% ethanol, and stored under refrigeration until squashed in 1% acetocarmine according to standard methods (Fukui and Nakayama, 1996). Chromosome numbers were documented with a camera lucida and photography with black and white film. For each individual, 5–30 cells with well-spread chromosomes were used for chromosome number determination. The numbers of individuals analyzed per population are given in Figs. 1 and 2 (showing number of individuals analyzed including previously published counts) and Table 1 (data presented here for the first time). Vouchers (Table 1) are on deposit in the herbarium of the Ohio State University (OS).

RESULTS

New counts for 292 plants from 105 populations of *Melampodium leucanthum* are reported (Table 1). These counts, together with previous reports (Stuessy, 1971a, b; Solbrig et al., 1972; Keil and Pinkava, 1976; Pinkava and Keil, 1977; Powell and Powell, 1977, 1978; Schaack, 1982; Strother, 1983; Ward, 1983), bring the total number of individuals investigated in this species to 440 plants from 188 populations (Fig. 1). In addition to sampling populations throughout the range of the taxon, we determined the occurrence of infrapopulational cytotype mixtures. The widespread cytological survey presented

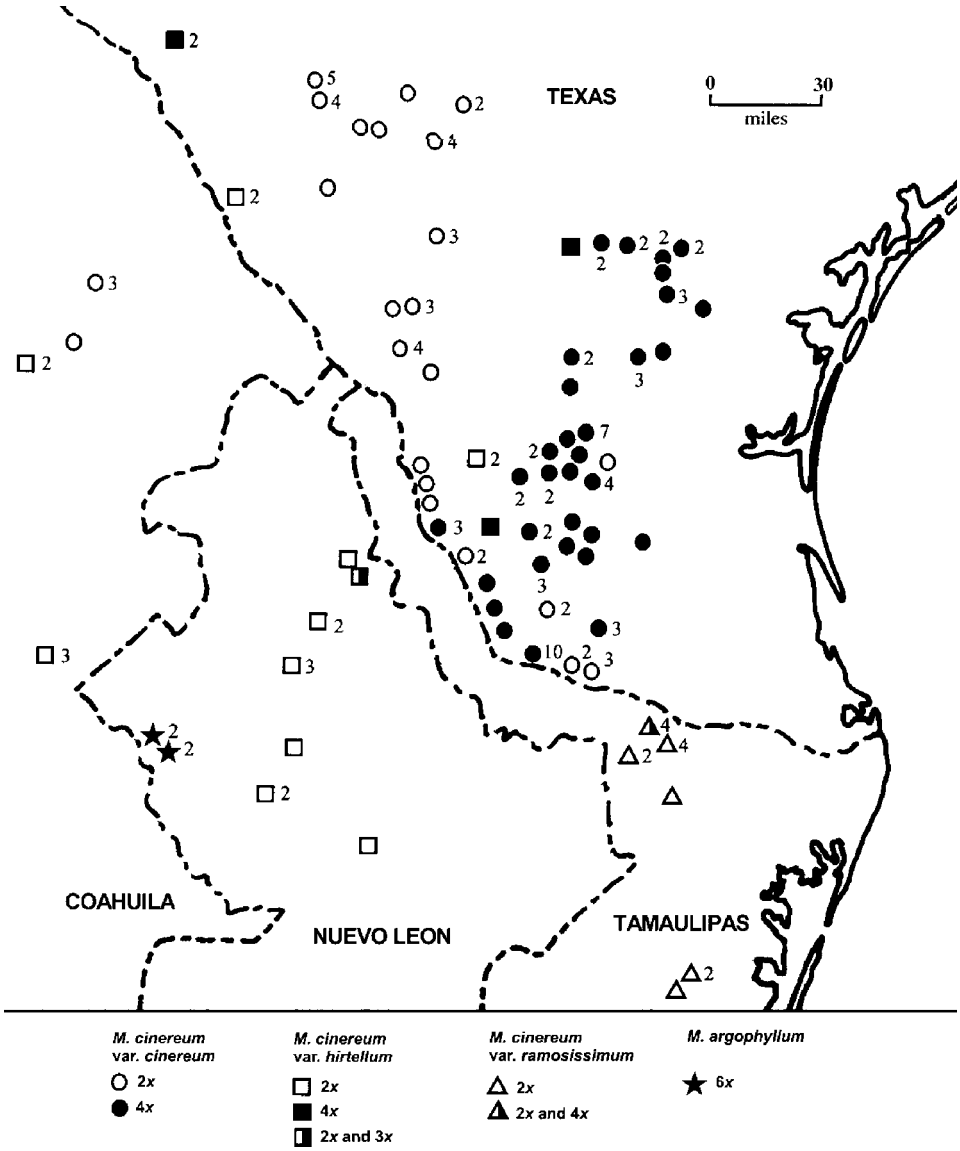

Fig. 2. Distribution in southern Texas and northeastern Mexico of chromosome counts in populations of *Melampodium cinereum* (var. *cinereum*, var. *hirtellum*, and var. *ramosissimum*). *Melampodium argophyllum* shown by stars ($n = 30$). Numbers indicate individuals counted in each population (if more than one). Data in part from Stuessy (1971a, b).

here for *Melampodium leucanthum* has continued to document the existence of both diploid ($n = 10$) and tetraploid ($n = 20$) individuals (Fig. 1). Meiotic irregularities occur commonly in tetraploids (cf. Table 1) and include presence of multivalents, univalents, bridges, laggards, and fragments. We did not, however, find any obvious geographical or ecological correlations. Tetraploids in *M. leucanthum* are centered in the Lampasas Plains and Edward's Plateau in the easternmost part of the range of the species. Populations with both 2*x* and 4*x* individuals have been detected, but they are not common (five populations: *SM 3546*, *SS 3622*, *SW 3553*, *SF 2004*, plus one population from Stuessy, 1971a; see Fig. 1). One 3*x* individual has been encountered in Blanco County, Texas (*SF 2005*; Fig. 1, inset).

New chromosome counts were obtained in 119 plants from 45 populations of *Melampodium cinereum*. These, added to the reports in Stuessy (1971a, b), bring the total number of counts for this species to 156 plants from 75 populations (Fig. 2). Three varieties are recognized within *M. cinereum* (Stuessy, 1972; Fig. 2). *Melampodium cinereum* var. *cinereum* is found mainly in the sandy plains of south-central Texas, variety *ramosissimum* in northeastern Mexico (mainly Tamaulipas) and adjacent Texas, and variety *hirtellum* in Coahuila, Nuevo León, and areas adjacent to the Rio Grande. Because of taxonomic complexity of the species, the cytological variation is reported independently for each variety.

Eighty-eight plants in 31 populations of *M. cinereum* var. *cinereum* have been newly analyzed (117 plants from 55 populations in total; Fig. 2). In most populations a single cytotype was recorded. Tetraploids are centered in the eastern portion of the range of var. *cinereum* and scattered along the Rio Grande. Diploids occur mostly in the western region, but are also intermixed with tetraploid populations to the south. No populations with cytotype mixtures or triploids have been detected.

TABLE 1. New chromosome counts (with locality and voucher) in the white-rayed complex of *Melampodium*. Letters after collection numbers (A, B, etc.) refer to counts from individual plants in that population. *F* = *Fischer*; *S* = *Stuessy*; *SF* = *Stuessy* & *Fischer*; *SM* = *Stuessy* & *Meacham*; *SS* = *T.* & *C. Stuessy*. Abbreviations of states according to Hollis and Brummitt (1992).

Taxon, locality, and vouchers[a]	*n* (no. of individuals; meiotic configurations)
M. argophyllum (A. Gray ex B.L. Rob.) S.F. Blake	
MEXICO	
NL. 29.7 mi SE of Coahuila border on Rte. 53, *SS 3599G*.	30 (1)
NL. 38.1 mi SE of Coahuila border on Rte. 53, *SS 3603A, B, D*.	30 (3)
M cinereum DC. var. *cinereum*	
MEXICO	
CO. 18.6 mi S of Allende, *SS 3593A–C*.	10 (3; one plant + 2B's)
USA	
TEX. Dimmit Co.: 6.3 mi N of Carrizo Springs, *SF 2031A*.	10 (1)
TEX. Frio Co.: ca. 8 mi S of Moore, *SS 3588A, C*.	10 (2)
TEX. Frio Co.: 1.7 mi W of Divot, *SS 3589A–D*.	10 (4; some I's)
TEX. Hildalgo Co.: 1.8 mi E of Sullivan City, *SF 2021A–C*.	10 (3)
TEX. La Salle Co.: near Cotulla, *SS 3619A–C*.	10 (3)
TEX. Starr Co.: 10 mi E of Rio Grande City, *SF 2023A, B*.	10 (2)
TEX. Starr Co.: 2.8 mi N of El Sauz, *SS 3614A, B*.	10 (2)
TEX. Uvalde Co., 8.9 mi S of Uvalde, *SF 2033A–E*.	10 (5)
TEX. Webb Co.: 1.8 mi NNW of jct Rtes. 35 & 83, *SF 2029*.	10 (3)
TEX. Webb Co.: 1 mi E jct Rtes. 44 & 83, *SF 2030 A–C*.	10 (3)
TEX. Zapata Co.: 0.2 mi SW of Zapata, *SF 2026 B, C*.	10 (2)
TEX. Zavala Co.: 11.9 mi S of Uvalde, *SF 2032A–D*.	10 (4)
TEX. Brooks Co.: 12.4 mi E of Hebbronville, *SF 2017A, C–E*.	20 (4)
TEX. Duval Co.: 30 mi N of Freer, *F 12*.	20 (1)
TEX. Duval Co.: 1.4 mi SW of San Diego, *SF 2013A, B, D*.	20 (3)
TEX. Duval Co.: 4.4 mi SW of Realitos, *SF 2015A, C–E, H, J, M*.	20 (7)
TEX. Duval Co.: 36.3 mi N of Hebbronville, *SS 3618A, B*.	20 (2; frags.)
TEX. Jim Hogg Co.: 2.3 mi W jct Rd 3073 and Rte. 16, *SF 2016A, C*.	20 (2)
TEX. Jim Hogg Co.: 15.8 mi S of Miranda City, *SS 3611A, B*.	20 (2)
TEX. Jim Hogg Co.: 8.4 mi S jct Rte. 16 & Rd 649, *SS 3612A, B*.	20 (2; 0–2 IV's)
TEX. Jim Hogg Co.: 7.9 mi N jct Rds 2686 & 649, *SS 3613A–C*.	20 (3)
TEX. Jim Hogg Co.: 4.9 mi S of Agua Nueva, *SS 3615A–C*.	20 (3)
TEX. Jim Hogg Co.: 20.8 mi N of Agua Nueva, *SS 3616B*.	20 (1)
TEX. Jim Hogg Co.: 1.5 mi N of Hebbronville, *SS 3617A*.	20 (1)
TEX. Jim Wells Co.: 30.7 mi S of George West, *SF 2010A–C*.	20 (3)
TEX. Jim Wells Co.: 8 mi W of Alice, *SF 2011A*.	20 (1)
TEX. Live Oak Co.: 7.4 mi S of George West, *SF 2009A, C*.	20 (2)
TEX. Starr Co.: ca. 0.5 mi E of Roma-Los-Saenz, *SF 2024A–E, K–O*.	20 (10; 12II + 1 ring IV + 3 chains IV)
TEX. Zapata Co.: 0.2 mi SSE of Lopeno, *SF 2025D*.	20 (1)
TEX. Zapata Co.: 3.8 mi NW of San Ygnacio, *SF 2027A–C*.	20 (3)
M. cinereum DC. var. *hirtellum* Stuessy	
MEXICO	
CO. 3 mi W of San Juan de Sabinas, *SS 3594A, C*.	10 (2)
CO. 22.9 mi S of Monclova, *SS 3597A–C*.	10 (3)
NL. ca. 50 mi S of Nuevo Laredo, *F 14*.	10 (1)
NL. 0.1 mi N of km 45 on Rte. 85, *F 17*.	10 (1)
NL. km 64 on Rte. 40 toward Reynosa, *F 19*.	10 (1)
NL. ca. 10 mi N of Monterrey, *SS 3605A, C*.	10 (2)
NL. ca. 63 mi N of Monterrey, *SS 3606A–C*.	10 (3; 4 frags.)
NL. 11.7 mi N of Sabinas Hidalgo, *SS 3608A, B*.	10 (2)
NL. 33.2 mi N of Sabinas Hidalgo, *SS 3609A, B*.	10 (1), 15 (1)
USA	
TEX. Maverick Co.: 8 mi S of Eagle Pass, *SS 3590A, C*.	10 (2)
TEX. Webb Co.: 20.5 mi E of Laredo, *SS 3610B, C*.	10 (2)
TEX. Kinney Co.: 10.9 mi W of Brackettville, *SF 2036B, D*.	20 (2)
M. cinereum DC. var. *ramosissimum* A. Gray	
MEXICO	
TA. ca. 5 mi SW of Reynosa, *SF 2018*.	10 (3; frags.), 20 (1)
TA. 2.6 mi S jct Rtes. 2 & 97, *SF 2020*.	10 (4)
M. leucanthum Torr & A. Gray	
USA	
COL. Pueblo Co.: 1.9 mi E of Colorado City, *SS, 2095A–C*.	10 (3)
COL. Pueblo Co.: 29.9 mi N of Walsenburg, *SS 2096A, C, D*.	10 (3)
NWM. Chaves Co.: 30.2 mi W of Caprock, *SM 3535A–C*.	10 (3)
NWM. Chaves Co.: 20.6 mi W of Caprock, *SM 3536A–C*.	10 (3)
NWM. Chaves Co.: 12.6 mi W of Caprock, *SM 3538A–C*.	10 (3)

TABLE 1. Continued.

Taxon, locality, and vouchers[a]	*n* (no. of individuals; meiotic configurations)
NWM. Chaves Co.: 5.7 mi S jct Rtes. 13 & 285, *SS 2088A–C*.	10 (3)
NWM. Colfax Co.: 2.7 mi N of Abbott, *SS 2092A*.	10 (1)
NWM. Colfax Co.: 12.3 mi W of Abbott, *SS 2093A–C*.	10 (3)
NWM. Otero Co.: 22 mi N of TEX-NWM line on Rte. 54, *SM 3531A–C*.	10 (3)
NWM. Roosevelt Co.: 8.8 mi NE of Elida, *SS 2089A–C*.	10 (3)
NWM. Quay Co.: 10 mi S of Logan, *SS 2091A, B*.	10 (2)
OKL. Ellis Co.: 12 mi N of Shattuck, *SS 3577A, C*.	10 (2)
TEX. Andrews Co.: 20.6 mi SW of Patricia, *SS 3552A–D*.	10 (4)
TEX. Andrews Co.: 4.5 mi SW of Andrews, *SW 3553A–C*.	10 (2); 20 (1; 40I)
TEX. Bailey Co.: 2.7 mi N jct Rd 37 & Rte. 214, *SM 3541A*.	10 (1)
TEX. Bailey Co.: 5.8 mi N jct Rd 37 & Rte. 214, *SM 3542A–C*.	10 (3)
TEX. Bailey Co.: 8.2 mi N of Needmore, *SM 3543A*.	10 (1)
TEX. Blanco Co.: 4 mi S of Johnson City, *SF 2004B, C*.	10 (1); 20 (1)
TEX. Blanco Co.: 5.2 mi N of Spring Branch, *SS 3622A–C*.	10 (2; 9II + 2I); 20 (1)
TEX. Brewster Co.: Marathon, *SF 2041A–D*.	10 (4)
TEX. Brewster Co.: 35.1 mi S of Marathon, *SS 2077A–C*.	10 (3)
TEX. Brewster Co.: 14.9 mi N of Study Butte, *SS 2083A–C*.	10 (3)
TEX. Briscoe Co.: 3.1 mi W of Quitaque, *SS 3562A–C*.	10 (3)
TEX. Carson Co.: 9.4 mi W of Pampa, *SS 3570A–C*.	10 (3)
TEX. Childress Co.: 15.2 mi E of Memphis, *SS 3563A*.	10 (1)
TEX. Coke Co.: 18.8 mi ENE of Sterling City, *SF 2058A–C*.	10 (3)
TEX. Concho Co.: 5.6 mi E of Eden, *SM 3509A–D*.	10 (4)
TEX. Crane Co.: 11.2 mi SW of Penwell, *SF 2054A–C*.	10 (3)
TEX. Crockett Co.: 21.2 mi S of Barnhart, *SM 3517A–C*.	10 (3)
TEX. Crockett Co.: 24.7 mi S of Ozona, *SM 3518A–C*.	10 (3)
TEX. Crockett Co.: 29 mi W of Ozona, *SS 2072A*.	10 (1)
TEX. Culberson Co.: 2.7 mi S of Van Horn, *SF 2045A–C*.	10 (3; frags.)
TEX. Culberson Co.: 0.6 mi S jct Rtes. 62 & 180, *SS 2086A–C*.	10 (3)
TEX. Dickens Co.: near Dickens, *SS 3559A–D*.	10 (4)
TEX. Donley Co.: 4 mi N of Brice, *SS 3565A, B, D*.	10 (3)
TEX. Donley Co.: 4.7 mi N of Clarendon, *SS 3566A*.	10 (1)
TEX. Ector Co.: W limits of Penwell, *SF 2055A–C*.	10 (3)
TEX. Gillespie Co.: 2.7 mi W of Fredericksberg, *SS 2071A, C*.	10 (2)
TEX. Glassock Co., 3.9 mi E of jct Rtes. 137 & 158, *SF 2057A–D*.	10 (4)
TEX. Gray Co.: 1.5 mi E of Lefors, *SS 3568A, C*.	10 (2)
TEX. Hansford Co.: 5.6 mi SE of Gruver, *SS 3574A–D*.	10 (4; some 9II + 2I)
TEX. Hartley Co.: 1.4 mi S of Dalhart, *SS 3572A–C*.	10 (3)
TEX. Hays Co.: 1.2 mi W of Henly, *SF 2003B, C*.	10 (2)
TEX. Hemphill Co.: 5.1 mi S of Canadian, *SS 3578A, B*.	10 (2)
TEX. Jeff Davis Co.: 7 mi S of Kent, *SS 2085A–C*.	10 (3)
TEX. Knox Co.: 13.5 mi S of Crowell, *SS 3580C*.	10 (1)
TEX. Lamb Co.: 15.2 mi N of Pettit, *SM 3540A–D*.	10 (4)
TEX. Lipscomb Co.: 3.9 mi WSW of Darrouzett, *SS 3576 A, C–E*.	10 (4; laggards, bridges)
TEX. Loving Co.: 1 mi SW of Mentone, *SF 2047A–C*.	10 (3)
TEX. Loving Co.: 12 mi E of Mentone, *SF 2048A–C*.	10 (3)
TEX. Lynn Co.: 5.5 mi S of New Moore, *SS 3551A, B*.	10 (2)
TEX. McCulloch Co.: 5.6 mi W of Brady, *SM 3508B–E*.	10 (4)
TEX. Medina Co.: 1.3 mi N jct Farm Rds 1283 & 471, *SF 2007A–C*.	10 (3)
TEX. Midland Co.: 10.4 mi ESE of Midland, *SF 2056A, B, D*.	10 (3)
TEX. Motley Co.: 18 mi N of Dickens, *SS 3560A–D*.	10 (4)
TEX. Motley Co.: 15.4 mi N of Matador, *SS 3561B, C*.	10 (2)
TEX. Ochiltree Co.: 27 mi E of Spearman, *SS 3575B–D*.	10 (3)
TEX. Oldham Co.: 6.8 mi NE of Vega, *SM 3545A–C*.	10 (3)
TEX. Oldham Co.: 14.1 mi NE of Vega, *SM 3546A, B, C*.	10 (2); 20 (1; bridges, frags.)
TEX. Parmer Co.: 18.3 mi N of Muleshoe, *SM 3544A*.	10 (1)
TEX. Pecos Co.: 20.2 mi W of Sanderson, *SF 2040A–C*.	10 (3)
TEX. Pecos Co.: 14.5 mi S of Ft. Stockton, *SM 3526A, C; SS 2076A, B*.	10 (2)
TEX. Pecos Co.: 4.9 mi E jct 67–385 on Rte. 290, *SS 2075A*.	10 (1)
TEX. Potter Co.: 14.9 mi SE jct Rte. 385 & Rch Rd 1061, *SM 3548A–C*.	10 (3)
TEX. Presidio Co.: 2.3 mi S of Marfa, *SF 2044A, C–I, K–R, T–W, X*.	10 (21; frags.)
TEX. Randall Co.: 2 mi N of Canyon, *SM 3549A–D*.	10 (4; 9II + 2I; 8II + 4I; laggards, micronuclei)
TEX. Randall Co.: 13.2 mi E of Canyon, *SM 3550A–C*.	10 (3)
TEX. Regan Co.: 9.5 mi E of Big Lake, *SM 3515B*.	10 (1)
TEX. Reeves Co.: 10 mi NNW of Pecos, *SF 2046A, C*.	10 (2)
TEX. Reeves Co.: 3 mi N of Balmorhea, *SM 3529A–D*.	10 (4)
TEX. Sherman Co.: near Stratford, *SS 3573A–C*.	10 (3)
TEX. Taylor Co.: 2 mi SW of Abilene, *SF 2095A–D*.	10 (4)
TEX. Tom Green Co.: 17.8 mi NW of San Angelo, *SM 3512B, C*.	10 (2; some 9II + 2I)

TABLE 1. Continued.

Taxon, locality, and vouchers[a]	*n* (no. of individuals; meiotic configurations)
TEX. Travis Co.: 5.2 mi W of Oak Hill, *SF 2002A*.	10 (1)
TEX. Uvalde Co.: 18.9 mi N of Uvalde, *SF 2034C*.	10 (1)
TEX. Uvalde Co.: 27.6 mi N of Uvalde, *SF 2035B–D*.	10 (3)
TEX. Val Verde Co.: 6 mi N of Del Rio, *SF 2037B, E*.	10 (2)
TEX. Val Verde Co.: 6.6 mi W of Comstock, *SM 3520A*.	10 (1)
TEX. Ward Co.: 16.1 mi SSW of Kermit, *SF 2050A–C*.	10 (3)
TEX. Yoakum Co.: 6.2 mi E of Plains, *SM 3539A*.	10 (1)
TEX. Blanco Co.: 1 mi N of Johnson City, *SF 2005A*.	15 (1)
TEX. Bell Co.: 6.2 mi W of Belton, *SF 2065B, C*.	20 (2)
TEX. Bexar Co.: 14.3 mi N of San Antonio, *SS 3621B*.	20 (1; 1–2 frags.)
TEX. Brown Co.: 3.1 mi ENE of Early, *SF 2062A–C*.	20 (3; 18II + 1IV)
TEX. Brown Co.: 6 mi S of May, *SS 3582B*.	20 (1; up to 7IV)
TEX. Brown Co.: 8.1 mi S of Brownwood, *SS 3583A, C*.	20 (2; 1–4IV)
TEX. Burnet Co.: 6.5 mi S of Burnet, *SF 2068A, D*.	20 (2)
TEX. Burnet Co.: 1.3 mi SE of Spicewood, *SF 2069A*.	20 (1; 15II + 1IV + 1VI)
TEX. Burnet Co.: 2.7 mi E of Bertram, *SM 3501B, C*.	20 (2; 16II + 2IV; 8II + 1IV)
TEX. Burnet Co.: 1.4 mi W of Burnet, *SM 3504A–C, E*.	20 (4; bridges)
TEX. Burnet Co.: 15.6 mi S of Lampasas, *SS 3587B*.	20 (1)
TEX. Coleman Co.: 5.5 mi SSE of Lawn, *SF 2060A, B, D*.	20 (3)
TEX. Coleman Co.: 9.1 mi SE of Coleman, *SF 2061A–D*.	20 (4; bridge + frags.; 14–20II + 0–3IV)
TEX. Comanche Co.: 1.9 mi SW of Lamkin, *SF 2063B, C*.	20 (2)
TEX. Coryell Co.: 11.9 mi NW of Gatesville, *SF 2064A–C*.	20 (3)
TEX. Hardeman Co.: 9.2 mi S of Quanah, *SS 3579B*.	20 (1; several multivalents)
TEX. Lampasas Co.: 9.6 mi E of Lampasas, *SF 2066B*.	20 (1)
TEX. Lampasas Co.: 2.2 mi S of Lampasas, *SF 2067A*.	20 (1)
TEX. Lampasas Co.: 2 mi S of Moline, *SS 3586A, B, D, F, G, K*.	20 (6; 4II + 8IV)
TEX. Medina Co.: 4.2 mi W of Mico, *SF 2008A, B, D*.	20 (3)
TEX. Mills Co.: 0.1 mi S of Goldthwaite, *SS 3584A–C*.	20 (3; some 2–3II or IV)
TEX. Travis Co.: 4.2 mi NW of Austin, *S 2000A*.	20 (1)
TEX. Travis Co.: 6.9 mi NW of Austin, *S 2001, SF 2070A*.	20 (1)
TEX. Val Verde Co.: 1 mi W of Pecos River on Rte. 90, *SF 2038A–C; SM 3521A–D, F*.	20 (3; 5)
TEX. Williamson Co.: 4.1 mi NNW of Leander, *SM 3500A–C*.	20 (3; 14–16II + 2–3IV)

[a] Conversion: 1 mi = 1.6 km.

Twenty-three plants in 12 populations of *M. cinereum* var. *hirtellum* have been newly analyzed (24 plants from 14 populations in total; Fig. 2). In 10 of the populations only diploids were recorded, all in the southern portion of the range of the taxon; three tetraploid populations were found in the northern and northeastern sectors. One population with one diploid and one triploid was found (*SS 3609*) in northern Nuevo León.

Eight plants in two populations of *M. cinereum* var. *ramosissimum* have been newly analyzed, and added to data in Stuessy (1970, 1971b), 14 individuals from six populations have been recorded (Fig. 2). In five of those populations only diploids were found; one population (*SF 2018*) had one tetraploid and three diploids (Fig. 2).

Melampodium argophyllum is restricted to the low mountains of northeastern Mexico (Stuessy, 1972) and has not previously been examined cytologically. We include it here for completeness of the cytological survey on the white-rayed complex. Results show only hexaploid ($n = 30$) cytotypes present in four plants from two populations of this species, suggesting that it might have been derived from diploid and tetraploid ancestors, perhaps via allopolyploidy.

DISCUSSION

Polyploids may be classified on the basis of their origin: autopolyploids arise within diploid taxa and allopolyploids are products of interspecific hybridization (Stebbins, 1971; Ramsey and Schemske, 1998). In some plant groups, particularly angiosperms, autopolyploids originate recurrently and are called neopolyploids (Soltis and Soltis, 1993; Ramsey and Schemske, 2002). New polyploid species are often adapted to new ecological conditions having a broader spectrum of tolerance (Levin, 1983, 2002), thus having new evolutionary potential.

Origin of tetraploids—Based on tetravalent formation during meiosis in tetraploids of both *Melampodium cinereum* and *M. leucanthum*, Stuessy (1971a) suggested their probable autopolyploid rather than allopolyploid origin. Results of the present survey add several dozens of new records of 4*x* plants having irregular pairing in meiosis (Table 1) and support that hypothesis. Presence of meiotic irregularities (multivalents, bridges) does not unambiguously indicate which type of polyploidization is operating, just as bivalent formation does not automatically support allopolyploidy. Bivalent promoting mechanisms (as suggested, e.g., for *Alopecurus bulbosus*; Sieber and Murray, 1980) or small chromosome size (e.g., *Arabidopsis*; Weiss and Maluszynska, 2000) can change the expected pairing behavior of polyploids. In *Melampodium*, in addition to the presence of meiotic irregularities, gross morphology of chromosomal races either does not differ at all (in *M. leucanthum*) or is manifested by quantitative morphological features only (in *M. cinereum* var. *cinereum*; Stuessy, 1971a). A diploid garden accession of *M. leucanthum* is reported to have given rise to tetraploid progeny (Turner and King, 1962).

The known distributions of chromosome races in *Melampodium leucanthum* and *M. cinereum* var. *cinereum*, with uniformly tetraploid populations in the eastern portion of these species ranges, and mixed 2*x*–4*x* populations isolated from the

main range of the tetraploids, is consistent with a recent, spontaneous, and recurrent autopolyploid formation. Polyploids may arise within otherwise diploid populations either through somatic chromosome doubling or, more commonly, through unreduced gametes (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998; Bretagnolle, 2001). Although no specific data bearing on these points exist for *Melampodium*, we suggest fusion of unreduced gametes, because it is the most common mechanism of polyploid formation (Levin, 2002).

Establishment, maintenance, and expansion of polyploids—The occurrence of cytotype mixtures at the infraspecific or even infrapopulational levels has been documented for plant species including mixtures of diploids and tetraploids (Dean and Chambers, 1983; Nicholson, 1983; Husband and Schemske, 1998) and/or higher level polyploid races (Stutz and Sanderson, 1983; Strother, 1989; Soejima, 1992; Weiss et al., 2002). The success of newly established polyploids within diploid populations depends on their fitness and ability to overcome the minority disadvantage, either by replacing diploids or spreading beyond their site(s) of origin and establishing a new populational system (Levin, 1983; Felber, 1991; Burton and Husband, 2000). If the two chromosomal races have different ecological preferences and tolerances, e.g., differences in germination, flowering times, or pollinators, they could coexist sympatrically (Fowler and Levin, 1984; Levin, 2002). The history of polyploid establishment in *Melampodium* might have followed the latter pathway. The distributional areas of 2*x* and 4*x* cytotypes in both taxa overlap only in small degree (Figs. 1, 2), being almost parapatric and suggesting differences in ecological tolerance. Once ''pure'' tetraploid populations have been successfully established in areas free from diploids, they might spread rapidly. This is perhaps what can be seen in *Melampodium cinereum* and *M. leucanthum*, especially in the latter where diploids occupy the majority of the species range, with tetraploids clustered in the eastern portion. A similar pattern of parapatric distribution has also been observed in *Chamerion* (*Epilobium*) *latifolium* (Mosquin and Small, 1971). The small number of populations containing both 2*x* and 4*x* cytotypes in *Melampodium leucanthum* and *M. cinereum* could be due to sampling errors. However, in one case 27 (Fig. 1) individuals were analyzed within a population (*SF 2044*), and no variation in chromosome number was encountered. Perhaps the polyploids, with a wider spectrum of tolerance, have adapted to ecological conditions not suitable for diploids (Levin, 1983). The small number of triploids suggests restriction of gene exchange, increasing reproductive isolation, and, in some cases, augmentation of morphological variation (e.g., quantitative differences in *M. cinereum* var. *cinereum*; Stuessy, 1971a).

Contact zones and hybridization—Chromosomal races of different ploidy levels may make contact along few to several hundred kilometers. These zones may result from secondary contact between previously allopatric chromosomal races (secondary contact zones; Petit et al., 1999) or the expansion of newly formed polyploids from within diploid populations. Contact zones usually lie along environmental interfaces, being maintained by selection against parental types in alien environments and hybrids/new cytotypes in parental environments (Hewitt, 1988). It is difficult to classify unambiguously the types of contact zones within the white-rayed complex of *Melampodium*. It seems plausible that these zones represent primary contacts, with tetraploids being formed recurrently within diploid populations (as seen in *M. leucanthum*) and spreading into new ecological niches, rather than outcompeting the diploids. It is possible that secondary contact zones exist. One population of *M. cinereum* var. *hirtellum* (*SS 3609*) with diploid and triploid individuals has been found in Nuevo León, suggesting ongoing hybridization between diploids and tetraploids. In this particular case no tetraploids have been found (Fig. 2). The contact zone between 2*x* and 4*x* in *M. leucanthum* is localized in the eastern part of its range. Four mixed populations were found (*SS 2004, M 3546, SS 3553, SS 3622*), and one population with a triploid individual was encountered in Blanco County, Texas (*SF 2005*). In proximity to that population, 2*x*, 4*x*, and mixed 2*x*–4*x* populations were found (Fig. 1, inset). Population density is high with all population types represented in this region. Two other 4*x* populations of *M. leucanthum* (*SS 3579, SF 2038* [=*3521*]) found in isolated positions in the middle of the 2*x* cytotype range suggest the recurrent formation of tetraploids within diploid populations rather than the presence of a contact zone. The contact zones in *Melampodium cinereum* var. *cinereum* and var. *hirtellum* are clearly distinguishable and lie in the center of the range of the species.

Contact zones with hybrids (*Chamerion* [*Epilobium*] *angustifolium*, Husband and Schemske, 1998; *Galax urceolata*, Burton and Husband, 1999; *Ixeris chinensis*, Pak et al., 1995; *Ranunculus ficaria*, Nicholson, 1983) and without hybrids (e.g., *Turnera sidioides*, Neffa and Fernández, 2001) have been documented. The fitness disadvantage of tetraploids in parental diploid populations may be reduced by partial viability and fertility of triploids as shown in the polyploid complex of *Chamerion* (*Epilobium*) *angustifolium* (Burton and Husband, 2000). Contact zones between cytotypes in the white-rayed species of *Melampodium* seem to be devoid of hybrids. The presence of only two populations with 3*x* (one individual in each; *SS 3609, SF 2005*) in all three species with more than 500 individuals analyzed suggests incompatibility of 2*x* and 4*x* plants and/or reproductive isolation, perhaps of an ecological or micro-phenotypic type. It is possible, however, that crosses may be occurring between 2*x* and 4*x* cytotypes, especially on the 4*x* level (i.e., via unreduced gametes in the diploid; e.g., deWet, 1980; Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998), which would be cytologically difficult to detect. In a polyploid *Draba* complex, polyploidy may help to overcome genetic depauperation caused by high rates of inbreeding at the 2*x* level (Brochmann, 1993). Whether similar mechanisms exist in *Melampodium* is not known. Preliminary experiments including cross- and self-pollination in a 4*x* population of *M. leucanthum* (*SF 2001*) indicate that some tetraploids are facultative outcrossers (T. F. Stuessy, unpublished data).

Polyploidization and speciation—Polyploidy is an important factor in plant speciation (Otto and Whitton, 2000; Ramsey and Schemske, 2002). Polyploids often undergo rapid structural and epigenetic changes that create new genetic entities (Raina et al., 1994; Matzke et al., 1999; Osborn et al., 2003). Species with inter- and infrapopulational cytotype mixtures are relatively common in certain groups of plants, including Asteraceae (e.g., Kay, 1969; Mooring, 1975, 1980; Semple, 1979; Chmielewski and Semple, 1983; Dean and Chambers, 1983; Soejima, 1992; Pak et al., 1995). Asteraceae are attractive for systematic studies due to their recent origin,

numerous species, and ease of karyological analyses. This plant family is still undergoing speciation, and polyploidy may be a mechanism that confers genetic novelty and enables processes of genome rearrangements to yield new genetic combinations. Polyploidy in certain species of *Melampodium* might have aided expansion of distributions of new taxa. One example (Stuessy and Brunken, 1979) is *M. microcephalum* ($n = 9$) and the related *M. paniculatum* ($n = 18$ and 27) in which the diploid is distributed in southern Mexico and polyploids in Central America and South America. The hexaploids of *M. argophyllum* may be another example of such a process. Formerly treated as a variety of *M. leucanthum* (Stuessy, 1969), it could have speciated after polyploidization involving either hybridization of tetraploids with diploids of the same or other species (possibly *M. cinereum*) and subsequent polyploidization or through autopolyploidization of tetraploids (e.g., fusion of unreduced 4*n* with 2*n* gametes; Weiss et al., 2002). This species is found in an ecologically and geographically distinct niche, in mountain ranges (1830–2440 m) distant from its closest relatives. Examples of higher polyploid formation within other species complexes have already been published, e.g., hexaploids of *Dalea formosa* (Fabaceae) are distributed in a large area among and beyond (to the south) diploids and tetraploids and might be the product of hybridization between 2*x* and 4*x* cytotypes, stabilized by polyploidization (Spellenberg, 1981).

Evolution and biogeography—A better understanding of chromosomal relationships in the white-rayed complex of *Melampodium* offers a chance to hypothesize on their origin and distributional relationships. Although speculative, these ideas offer a framework for future testing with molecular (and other) data. Stuessy (1971a, 1979) suggested that the white-rayed complex must have been derived from the yellow-rayed portion of the genus. The white-rayed complex is adapted to xeric conditions and occurs at the northernmost extreme of distribution. We suggest that an ancestral white-rayed taxon originated from the immediate ancestor of the diploid, yellow-rayed, shrubby *M. americanum* L. of the same taxonomic section (Stuessy, 1972). The modern range of *M. americanum* extends from Guatemala to northern Mexico (Stuessy, 1972).

As the Pleistocene came to a close (approximately 12 000 years ago), further divergence in the white-rayed complex might have occurred as the region became drier and warmer (Van Devender, 1980; Wells, 1983; Van Devender and Wiens, 1993). Drying of valleys between mountains might have correlated with the movement of some plant populations from lower to higher sites and others to more northerly regions. *Melampodium cinereum* could have developed more fully northeastward near the Rio Grande. *Melampodium leucanthum* may have evolved in isolated mountains to the west of *M. cinereum* in Coahuila, Mexico. Hybridization between the two early populational derivatives, followed by polyploidization, could have yielded *M. argophyllum*, a hexaploid, which survives today, perhaps relictually, only in isolated populations in higher mountains (above 1830 m; Stuessy, 1972) abutting the westernmost edge of the range of *M. cinereum* and the southernmost edge of *M. leucanthum*. The two parental diploid taxa could have continued their range extensions, with the former reaching to the Rio Grande and the latter extending northward through the Big Bend of Mexico and Texas into northern Texas and adjacent Colorado, Kansas, and Oklahoma, and westward to New Mexico and Arizona. Autopolyploidy could have occurred frequently within both developing *M. cinereum* and *M. leucanthum*. In the case of *M. leucanthum*, the recurring 4*x* cytotypes were apparently unable to develop racial status within parental diploid areas, except for those that originated on the uplifted limestone bedrock of Edwards's Plateau in central Texas, which has a strong impact on plant distributions and harbors 76 endemic vascular plant taxa (Amos and Rowell, 1988). Once tetraploids occurred in the region tolerated less well by diploids, they might have become established and colonized successfully. Within *M. cinereum*, colonizing populations might have diverged morphologically to some extent (to such a degree that they are now recognized taxonomically as varieties; Stuessy, 1972) and, again, autopolyploidy may have given rise to 4*x* populations that eventually established on the northeastern periphery of the range of the species. Quantitative morphological divergence between the cytotypes of *M. cinereum* var. *cinereum* may indicate that they differentiated earlier than those in *M. leucanthum*. The Edward's Plateau may have served as barrier to further northward migration of *M. cinereum*; no hybrids between *M. cinereum* and *M. leucanthum* have ever been reported, nor have any hybrids been found in the contact zone between the two taxa (T. F. Stuessy, personal observations).

LITERATURE CITED

AMOS, B. B., AND C. M. ROWELL, JR. 1988. Floristic geography of woody and endemic plants. *In* B. B. Amos and F. R. Gehlbach [eds.], Edwards Plateau vegetation: plant ecological studies in central Texas, 25–42. Baylor University Press, Waco, Texas, USA.

BEVER, J. D., AND F. FELBER. 1992. The theoretical population genetics of autopolyploidy. *Oxford Surveys in Evolutionary Biology* 8: 185–217.

BRETAGNOLLE, F. 2001. Pollen production and spontaneous polyploidization in diploid populations of *Anthoxanthum odoratum*. *Biological Journal of the Linnean Society* 72: 241–247.

BRETAGNOLLE, F., AND J. D. THOMPSON. 1995. Gametes with the somatic chromosome number: mechanisms of their formation and role in the evolution of polyploid plants. *New Phytologist* 129: 1–22.

BROCHMANN, C. 1993. Reproductive strategies of diploid and polyploid populations of arctic *Draba* (Brassicaceae). *Plant Systematics and Evolution* 185: 55–83.

BURTON, T. L., AND B. C. HUSBAND. 1999. Population cytotype structure in the polyploid *Galax urceolata* (Diapensiaceae). *Heredity* 82: 381–390.

BURTON, T. L., AND B. C. HUSBAND. 2000. Fitness differences among diploids, tetraploids, and their triploid progeny in *Chamerion angustifolium*: mechanisms of inviability and implications for polyploid evolution. *Evolution* 54: 1182–1191.

CHMIELEWSKI, J. G., AND J. C. SEMPLE. 1983. The cytogeography of *Aster lanceolatus*. III. Cytoecology in Southern Ontario. *Canadian Journal of Botany* 61: 1879–1886.

DEAN, M. L., AND K. L. CHAMBERS. 1983. Chromosome numbers and evolutionary patterns in the *Aster occidentalis* (Asteraceae) polyploid complex of western North America. *Brittonia* 35: 189–196.

DEWET, J. M. J. 1980. Origins of polyploids. *In* W. H. Lewis [ed.], Polyploidy—biological relevance, 3–16. Plenum, New York, New York, USA.

FELBER, F. 1991. Establishment of a tetraploid cytotype in a diploid population: effect of relative fitness of the cytotypes. *Journal of Evolutionary Biology* 4: 195–207.

FOWLER, N. L., AND D. A. LEVIN. 1984. Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. *American Naturalist* 124: 703–711.

FUKUI, K., AND S. NAKAYAMA [EDS.]. 1996. Plant chromosomes. Laboratory methods. CRC Press, Boca Raton, Florida, USA.

GOLDBLATT, P. 1980. Polyploidy in angiosperms. *In* W. H. Lewis [ed.], Polyploidy—biological relevance, 219–239. Plenum, New York, New York, USA.

HEWITT, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* 3: 158–167.

HOLLIS, S., AND R. K. BRUMMITT. 1992. World geographical scheme for recording plant distributions. Plant taxonomic database standards no. 2. International Working Group on Taxonomic Databases for Plant Sciences (TDWG), Hunt Institute for Botanical Documentation, Pittsburgh, Pennsylvania, USA.

HUSBAND, B. C., AND D. W. SCHEMSKE. 1998. Cytotype distribution at a diploid-tetraploid contact zone in *Chamerion* (*Epilobium*) *angustifolium* (Onagraceae). *American Journal of Botany* 85: 1688–1694.

JACKSON, R. C., AND J. CASEY. 1982. Cytogenetic analyses of autopolyploids: models and methods for triploids to octoploids. *American Journal of Botany* 69: 487–501.

JACKSON, R. C., AND D. P. HAUBER. 1982. Autotriploid and autotetraploid cytogenetic analyses: correction coefficients for proposed binomial models. *American Journal of Botany* 69: 644–646.

KAY, Q. O. N. 1969. The origin and distribution of diploid and tetraploid *Tripleurospermum inodorum* (L.) Schultz Bip. *Watsonia* 7: 130–141.

KEIL, D. J., AND D. J. PINKAVA. 1976. Chromosome counts and taxonomic notes for Compositae from the United States and Mexico. *American Journal of Botany* 63: 1393–1403.

LEITCH, I. J., AND M. D. BENNETT. 1997. Polyploidy in angiosperms. *Trends in Plant Science* 2: 470–476.

LEVIN, D. A. 1975. Minority cytotype exclusion in local plant populations. *Taxon* 24: 35–43.

LEVIN, D. A. 1983. Polyploidy and novelty in flowering plants. *American Naturalist* 122: 1–25.

LEVIN, D. A. 2002. The role of chromosomal change in plant evolution. Oxford University Press, New York, New York, USA.

MATZKE, M. A., O. MITTELSTEN-SCHEID, AND A. J. M. MATZKE. 1999. Rapid structural and epigenetic changes in polyploid and aneuploid genomes. *BioEssays* 21: 761–767.

MCARTHUR, E. D., AND S. C. SANDERSON. 1999. Cytogeography and chromosome evolution of subgenus Tridentatae of *Artemisia* (Asteraceae). *American Journal of Botany* 86: 1754–1775.

MOORING, J. S. 1975. A cytogeographic study of *Eriophyllum lanatum* (Compositae, Helenieae). *American Journal of Botany* 62: 1027–1037.

MOORING, J. S. 1980. A cytogeographic study of *Chaenactis douglasii* (Compositae, Helenieae). *American Journal of Botany* 67: 1304–1319.

MOSQUIN, T., AND E. SMALL. 1971. An example of parallel evolution in *Epilobium* (Onagraceae). *Evolution* 25: 678–682.

NEFFA, V. G. S., AND A. FERNANDEZ. 2001. Cytogeography of the South American *Turnera sidoides* L. complex (Turneraceae, Leiocarpae). *Botanical Journal of the Linnean Society* 137: 189–196.

NICHOLSON, G. G. 1983. Studies on the distribution and the relationship between the chromosome races of *Ranunculus ficaria* L. in S.E. Yorkshire. *Watsonia* 14: 321–328.

OSBORN, T. C., J. C. PIRES, J. A. BIRCHLER, D. L. AUGER, Z. J. CHEN, H.-S. LEE, L. COMAI, A. MADLUNG, R. W. DOERGE, V. COLOT, AND R. A. MARTIENSSEN. 2003. Understanding mechanisms of novel gene expression in polyploids. *Trends in Genetics* 19: 141–147.

OTTO, S. P., AND J. WHITTON. 2000. Polyploid incidence and evolution. *Annual Reviews of Genetics* 34: 401–437.

PAK, J.-H., N.-C. KIM, K. CHOI, I.-S. KIM, B.-B. SEO, AND S.-D. SONG. 1995. Geographical distributions of diploids, triploids, and tetraploids of the *Ixeris chinensis* complex (Asteraceae: Lactuceae) of South Korea. *Korean Journal of Plant Taxonomy* 25: 221–236.

PETIT, C., F. BRETAGNOLLE, AND F. FELBER. 1999. Evolutionary consequences of diploid-polyploid hybrid zones in wild species. *Trends in Ecology and Evolution* 14: 306–311.

PINKAVA, D. J., AND D. J. KEIL. 1977. Chromosome counts of Compositae from the United States and Mexico. *American Journal of Botany* 64: 680–686.

POWELL, A. M., AND S. A. POWELL. 1977. Chromosome numbers of gypsophilic plant species of the Chihuahuan Desert. *Sida* 7: 80–90.

POWELL, A. M., AND S. A. POWELL. 1978. Chromosome numbers in Asteraceae. *Madroño* 25: 160–169.

RAINA, S. N., A. PARIDA, K. K. KOUL, S. S. SALIMATH, M. S. BISHT, AND V. RAJA. 1994. Associated chromosomal DNA changes in polyploids. *Genome* 37: 560–564.

RAMSEY, J., AND D. W. SCHEMSKE. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29: 467–501.

RAMSEY, J., AND D. W. SCHEMSKE. 2002. Neopolyploidy in flowering plants. *Annual Review of Ecology and Systematics* 33: 589–639.

RODRIGUEZ, D. J. 1996. A model for the establishment of polyploidy in plants. *American Naturalist* 147: 33–46.

SCHAACK, C. G., R. HERLY, AND M. L. RUSCHE. 1982. *In* Á. Löve [ed.], IOPB chromosome number reports LXXV. *Taxon* 31: 366–367.

SEMPLE, J. C. 1979. The cytogeography of *Aster lanceolatus* (synonyms *A. simplex* and *A. paniculatus*) in Ontario with additional counts from populations in the United States. *Canadian Journal of Botany* 57: 397–402.

SIEBER, V. K., AND B. G. MURRAY. 1980. Spontaneous polyploids in marginal populations of *Alopecurus bulbosus* Gouan (Poaceae). *Botanical Journal of the Linnean Society* 81: 293–300.

SOEJIMA, A. 1992. Taxonomical study of *Aster leiophyllus* complex (Compositae) in Kanto District, Japan, with special reference to ploidy level. *Botanical Magazine Tokyo* 105: 13–28.

SOLBRIG, O. T., D. W. KYHOS, A. M. POWELL, AND P. H. RAVEN. 1972. Chromosome numbers in Compositae VIII: Heliantheae. *American Journal of Botany* 59: 869–878.

SOLTIS, D. E., AND P. S. SOLTIS. 1993. Molecular data and the dynamic nature of polyploidy. *Critical Reviews in Plant Sciences* 12: 243–273.

SOLTIS, D. E., AND P. S. SOLTIS. 1999. Polyploidy: recurrent formation and genome evolution. *Trends in Ecology and Evolution* 14: 348–352.

SOLTIS, P. S., AND D. E. SOLTIS. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proceedings of the National Academy of Sciences USA* 97: 7051–7057.

SPELLENBERG, R. 1981. Polyploidy in *Dalea formosa* (Fabaceae) on the Chihuahuan Desert. *Brittonia* 33: 309–324.

STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold, London, UK.

STROTHER, J. L. 1983. More chromosome studies in Compositae. *American Journal of Botany* 70: 1217–1224.

STROTHER, J. L. 1989. Chromosome numbers in *Thymophylla* (Compositae: Tageteae). *Sida* 13: 351–358.

STUESSY, T. F. 1969. A new variety and new combination in *Melampodium* (Compositae-Heliantheae). *Sida* 3: 348–349.

STUESSY, T. F. 1970. Chromosome studies in *Melampodium* (Compositae, Heliantheae). *Madroño* 20: 365–37.

STUESSY, T. F. 1971a. Systematic relationships in the white-rayed species of *Melampodium* (Compositae). *Brittonia* 23: 177–190.

STUESSY, T. F. 1971b. Chromosome numbers and phylogeny in *Melampodium* (Compositae). *American Journal of Botany* 58: 732–736.

STUESSY, T. F. 1972. Revision of the genus *Melampodium* (Compositae: Heliantheae). *Rhodora* 74: 1–70; 161–219.

STUESSY, T. F. 1979. Cladistics of *Melampodium* (Compositae). *Taxon* 28: 179–195.

STUESSY, T. F., AND J. N. BRUNKEN. 1979. Artificial interspecific hybridization in *Melampodium* section *Zarabellia* (Compositae). *Madroño* 26: 53–63.

STUTZ, H. C., AND S. C. SANDERSON. 1983. Evolutionary studies of *Atriplex*: chromosome races of *A. confertifolia* (shadscale). *American Journal of Botany* 70: 1536–1547.

SUNDBERG, S. D., AND T. F. STUESSY. 1990. Isolating mechanisms and implications for modes of speciation in Heliantheae (Compositae). *In* T. J. Mabry and G. Wagenitz [eds.], Research advances in the Compositae, 77–97. Springer-Verlag,Vienna, Austria.

TURNER, B. L. 1988. A new species of *Melampodium* (Asteraceae-Heliantheae) from Oaxaca, Mexico. *Phytologia* 64: 445–447.

TURNER, B. L. 1993. A new species of *Melampodium* (Asteraceae, Heliantheae) from Jalisco, Mexico. *Phytologia* 75: 136–139.

TURNER, B. L., AND D. FLYR. 1966. Chromosome numbers in the Compositae. X. North American species. *American Journal of Botany* 53: 24–33.

TURNER, B. L., AND R. M. KING. 1962. A cytotaxonomic survey of *Melampodium* (Compositae, Heliantheae). *American Journal of Botany* 49: 263–269.

VAN DEVENDER, T. R. 1980. Holocene plant remains from Rocky Arroyo and Last Chance Canyon, Eddy County, New Mexico. *Southwestern Naturalist* 25: 361–372.

VAN DEVENDER, T. R., AND J. F. WIENS. 1993. Holocene changes in the flora of Ragged Top, South-central Arizona. *Madroño* 40: 246–264.

WARD, D. E. 1983. Chromosome counts from New Mexico and Southern Colorado. *Phytologia* 54: 302–309.

WEISS, H., C. DOBEŠ, G. M. SCHNEEWEISS, AND J. GREIMLER. 2002. Occurrence of tetraploid and hexaploid cytotypes within and between popu-

lations in *Dianthus* sect. *Plumaria* (Caryophyllaceae). *New Phytologist* 156: 85–94.

WEISS, H., AND J. MALUSZYNSKA. 2000. Chromosomal rearrangement in autotetraploid plants of *Arabidopsis thaliana*. *Hereditas* 133: 255–261.

WELLS, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs* 53: 341–382.

WENDEL, J. F. 2000. Genome evolution in polyploids. *Plant Molecular Biology* 42: 225–249.