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GENETICAL POPULATION STRUCTURE IN PLANTS: GENE FLOW BETWEEN DIPLOID SEXUAL AND TRIPLOID ASEXUAL DANDELIONS (*TARAXACUM* SECTION *RUDERALIA*)

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Abstract.—Levels and distribution of genetic variation were studied in central and western European populations of *Taraxacum* section *Ruderalia* containing differing mixtures of sexual diploid and asexual triploid plants. All sexual populations were panmictic with their variation partitioned mainly among populations. Genotypic diversity in triploid samples was very high with few clones widespread and many clones restricted to one or a few populations. Extensive amounts of gene (pollen) flow between the diploid and triploid components of a population were inferred from the following data: (1) the two ploidy levels share all major allozyme polymorphisms; (2) the intrapopulational homogeneity in genic variation between diploids and triploids contrasts strongly with the geographic differentiation at each ploidy level separately; (3) population-unique alleles simultaneously occur at the two ploidy levels; (4) not only sexuals but also asexuals generally simulate Hardy-Weinberg expectations. Most likely, intrapopulational gene exchange occurs bidirectionally by mechanisms such as reductional pollen meiosis in apomictic plants, facultative apomixis, and formation of unreduced gametes in sexuals. Thus, diploid and triploid *Taraxacum* section *Ruderalia* are less genetically isolated than has previously been supposed and probably form a cohesive evolutionary unit with the level at which gene pools are shared differing by population.

Key words.—Allozymes, apomixis, clonal variation, dandelions, multilocus genotypes, pollen flow, *Taraxacum.*

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The evolutionary potential of a population or species depends largely on levels and patterns of genic variation. The amount of variation is determined by effective population size, historical events, mating system(s), and population structure. The distribution patterns of variability are the outcome of a variety of population parameters. Roughly speaking, little gene flow, small population size, and differing selection pressures promote population differentiation, whereas much gene flow, large population sizes, and uniform selection regimes produce spatially homogeneous patterns of variation. Among the complex interactions of these stochastic and deterministic forces, gene flow is of prime importance for shaping the genetical structure both within and among populations (Endler 1977; Turner et al. 1982). Earlier suggestions that gene flow in plants is very limited (Levin and Kerster 1969; Schaal 1980) are now being challenged (Levin 1981; Smyth and Hamrick 1987; Devlin and Ellstrand 1990).

The genus *Taraxacum* (dandelions) is noted for its taxonomic complexity, which to a great extent is associated with the occurrence of various breeding systems and ploidy levels (Richards 1986). In *Taraxacum* section *Ruderalia,* formerly called *Vulgaria,* diploid ($2n = 16$) species make up less than 10% of the total number; they reproduce obligatorily sexually, and normally are self-incompatible. Some 2000 *Ruderalia* microspecies have been described, which are all apomictic (also called agamospermous) triploids ($2n = 24$). They reproduce through diplosporic gametophytic apomixis of the *Taraxacum* type (Asker and Jerling 1992, p. 53); this means that embryo development commences without any influence of the pollen tube (i.e., nonpseudogamy). Higher ploidy levels are rare. Like most clonally structured plant populations (Ellstrand and Roose 1987), apomictic *Taraxacum* microspecies are generally composed of a number of clones, only a few of which are widespread (Van Oostrum et al. 1985; Hughes and Richards 1988; Battjes et al. 1992; for uniclonal species see the last reference and Menken and Morita 1989).

Strict apomixis supposedly brings about complete reproductive isolation; on this fact the microspecies concept in *Taraxacum* is based. New triploids may arise through simple mutation, chromosome loss or gain, and somatic recombination (Richards 1989); triploids might also be derived from matings between diploids involving unreduced meiotic products (Harlan and deWet 1975; Jenniskens 1984). Some studies, however, have supported the idea of the production of new genetic combinations at both ploidy levels through bidirectional gene exchange between diploids and triploids. For instance, Sørensen and Gudjonsson (1946) found partial return to sexuality in some hypoploid ($2n = 23$) plants. Furthermore, in field and greenhouse experiments in which triploids were used to pollinate diploids, a complex mixture of diploid, triploid, tetraploid, and aneuploid progeny was encountered (Müller 1972; Sterk 1987), although seed set was significantly lower than after cross-pollination by other diploids. It appears that in anthesis of most if not all facultative and obligate agamosperms, meiosis is reductional but disturbed, producing aneuploid as well as eu-haploid, eu-diploid, and eu-triploid pollen (Richards 1973), thus explaining the wide range of ploidy types in the aforementioned F_1 progeny. Only facultative agamosperms also exhibit partially regular meiosis in ovule formation. This was supported by the occurrence of diploid progeny in crosses between triploid mother and diploid father plants (Richards 1970a; Múller 1972). However, transmission of paternal genes could unequivocally be proved by means of genetic markers in only a few cases (Hughes and Richards 1988; Morita et al. 1990).

TABLE 1. Location, percentage (average of two estimates in nonconsecutive years) diploids, and numbers of diploid and triploid individuals analyzed in populations of *Taraxacum*. A, Austria; G, Germany; F, France; N, the Netherlands. Reference and code number refer to the original studies concerning first census estimates of diploids and site descriptions: 1, Den Nijs and Sterk 1984b; 2, Den Nijs and Sterk 1984a; and 3, Den Nijs and Sterk 1980; 4, Den Nijs et al. 1990; 5, Elzinga et al. 1987; 6, unpubl. data.

Designation	Locality	Reference	Code no.	Diploid (%) (mean)	No. of plants analyzed	
					Diploids	Triploids
T1	Strazeele (F)	1	TPH 1	65	32	—
T2	La Chapelle-sur-Aveyron (F)	2	THM 83	25	57	14
T3	Villeuch (F)	2	THM 116	75	38	—
T4	Sainte Hermine (F)	2	THM 95	100	46	—
T5	Saint Léonard-de-Noblat (F)	2	THM 43	90	67	—
T6	Villefranche-de-Rouergue (F)	2	THM 35	60	34	24
T7	Saint Jean-du-Gard (F)	2	THM 26	90	34	—
T10	Belleville (F)	2	THM 13	45	42	36
T11	Corveissiat (F)	2	THM 50	30	11	53
T13	Wolschwiller (F)	3	17	85	39	—
T19	Rapottenstein (A)	3	52	90	35	29
T20	Odenwald (G)	6	*	60	29	15
T22	Gut am steg (A)	3	1	80	75	—
T23	Salem (G)	3	TP 1	100	28	—
T24	Jauerling (A)	3	3	80	50	—
T25	Kaumberg (A)	3	4	45	25	38
T26	Lunz-Seehof (A)	3	7	100	55	—
T27	Bad-Pirawarth (A)	4	—	80	53	11
T28	Amstetten (A)	4	—	60	36	—
T30	Mechelen, South Limburg (N)	5	1	30	35	30
TB1	Valkenburg, South Limburg (N)	6	†	50	64	—
TCB	ibidem	6	†	<5	—	45
TCC	ibidem	6	†	<5	—	79

* T20, Odenwald, Ellerbach Valley: west-exposed grassland on "Buntsandstein," ca. 25 yr old, moderately manured with stable dung and fertilizer; ca. 300 m above sea level.

† TB1/TCB/TCC, Valkenburg: pastures, ca. 20 ha area, until recently heavily manured, slightly east exposed; ca. 150 m above sea level.

Quite surprisingly, in greenhouse experiments pollen from triploids also is able to induce self-fertilization in normally self-incompatible diploids (Menken et al. 1989; Morita et al. 1990). Self-fertilization otherwise is a rare phenomenon in diploid *Taraxacum,* except for species in the small sections *Leptocephala* and *Serotina* (Doll 1977), and at very low frequencies or as "end-of-flowering-period" phenomenon in other sections of *Taraxacum* (Warmke 1944; Jenniskens 1984). Finally, spontaneous hybridization between species both within and between sections was observed in certain areas (Fürnkranz 1966; Richards 1970b). Considering all these possible mechanisms, de novo formation of diploid and triploid plants in mixed natural populations is expected.

The impact of the phenomena mentioned above was assumed to be quite local, mainly as a consequence of the relict distribution of sexual diploids and the resulting rareness of mixed populations (Van Soest 1958; Fürnkranz 1966; Richards 1973). Extensive cytogeographical studies, however, revealed that diploids are widely spread over large parts of central and western Europe where they generally cooccur with triploids (Den Nijs and Sterk 1980, 1984a,b; Den Nijs et al. 1990; Den Nijs and Menken 1994). The diploid/triploid ratio varies by population (see table 1), occasionally pure diploid or triploid populations can be found. In southern Bavaria and western Czechoslovakia as well as north and south of this area, diploids are essentially lacking, this giving a disjunct western and eastern mixed distribution area (hereafter abbreviated as WMA and EMA, respectively; fig. 1).

Apomictic *Taraxacum* section *Ruderalia* species have a larger range than closely related sexuals (Mogie and Ford 1988; Den Nijs and Menken 1994), a phytogeographical pattern similar to that observed in other agamic complexes (so-called geographic parthenogenesis; Vandel 1928; Bierzychudek 1987). It appears that apomicts have larger ecological tolerances than their sexual progenitors probably because of (1) a hybrid and polyploid nature, combining or even exceeding the progenitors' ecological ranges and (2) the (near) absence of recombination such that a genotype doing well in a certain environment can produce equally well-adapted progeny (Bierzychudek 1989). Yet, in mixed areas, sexuals and triploids appear to occupy similar habitat ranges. Mogie and Ford (1988) developed a scenario in which long distance dispersal with the retreat of the glaciers favored the spread of apomicts. Because sexuals are normally self-incompatible and require insect-mediated pollination whereas apomicts produce seeds without pollination, during low-density colonization episodes apomicts will increase in numbers more quickly than sexuals. Moreover, in this situation, sexuals would be likely to receive pollen from apomicts thereby forming sexual diploid as well as asexual progeny and helping to produce a growing number of triploids (Richards 1973). However, if sexuals have a selective advantage over asexuals (e.g., in complex ecosystems or at xerothermic sites) this process may be reversed (Sterk 1987; Elzinga et al. 1987); in addition, sexually reproducing organisms are usually thought to outcompete strict agamosperms in the long run. Therefore, the aim of the present study was to analyze the composition and distribution of genetic variation both within and among mixed populations of diploid and triploid *Taraxacum* section *Ruderalia* and to determine indirectly the

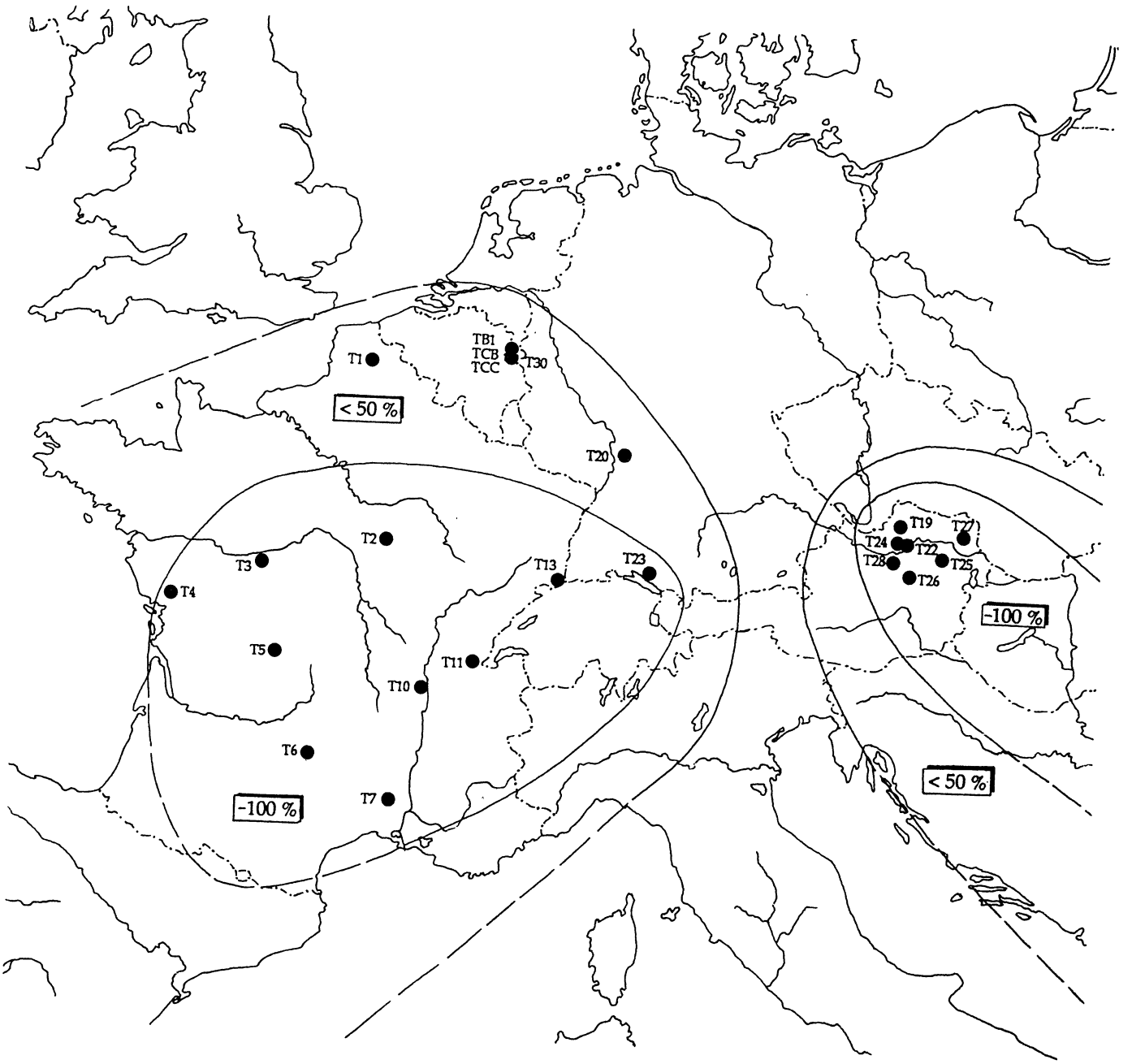

FIG. 1. Collection localities of *Taraxacum* section *Ruderalia* in western and central Europe and a rough indication of the distribution of diploids and their percentages of occurrence.

occurrence and extent of gene flow between the two ploidy levels.

MATERIALS AND METHODS

In spring 1985, dandelions were sampled as roots in 23 populations (pastures) distributed over western and central Europe (fig. 1) and grown in the greenhouse in Amsterdam. Sample sites, number of diploid and triploid plants analyzed, and field-estimated population ratio of diploid/triploid plants are listed in table 1. Sampling was somewhat biased towards diploids (table 1) for reasons connected with other experiments. Ploidy levels of individual plants were established by pollen-diameter analysis (Morita 1976; Den Nijs and Sterk 1980). Acknowledging that the reliability of this technique for estimates of diploid/triploid ratios is somewhat questionable (a once-only sample, whereas diploids and triploids may flower asynchronously to a certain extent), ploidy ratios were estimated in a non-consecutive year, and the average is given in table 1.

Initially, ploidy levels of individual plants that were used in the allozyme analyses were randomly verified in a number of samples by counting chromosomes in aceto-orcein root-

tip squash preparations. The frequency of misclassification in these plants was less than 10%. The great majority of misclassified plants had pollen patterns that fell in between those of pure diploid and pure triploid individuals. In the course of the study, all plants with such intermediate pollen patterns were cytologically checked, as were plants with zymograms that were inconsistent between loci.

Electrophoresis

Protein extraction, electrophoresis, enzyme assays, and isozyme and allozyme specifications followed Menken et al. (1989); analyses were performed in 1985 and 1986. From an initial screening of 15 enzyme systems (Menken et al. 1989), only 6-phosphogluconate dehydrogenase (6PGDH-1 and 6PGDH-2, being the cytosolic and chloroplastic forms, respectively) and malate dehydrogenase (MDH) were used. These three enzymes were suitably polymorphic and consistently interpretable in space and time; every plant was electrophoresed twice, 2–3 wk apart, and those with inconsistent patterns were discarded. Moreover, all are dimeric enzymes; thus, in the absence of dosage compensation (Ciferri et al. 1969; Roose and Gottlieb 1980), they allow straightforward genotyping of both kinds of heterozygous triploids. The loci are located in the nuclear DNA, inherited in a simple Mendelian fashion, and are unlinked (Menken et al. 1989). If triploid plants showed regular diploid heterozygous patterns, a null allele was designated. Only populations with sample sizes exceeding ten per ploidy level were used in the calculations.

Data Analysis

Diversity among asexuals was described as (1) proportion distinguishable (being the number of clones encountered divided by sample size; a value of 1.00 means every individual has a unique genotype) and (2) clonal diversity ($H_g = 1 - \Sigma p_i^2$, p_i being the frequency of the ith clone in a sample). Individuals were assigned to the same clone if they shared an identical three-locus phenotype. Clonal equitability (evenness) was calculated as the effective number of clones divided by the number of clones, $(1/\Sigma p_i^2)/N_c$. This is a relative measure that can be used to compare samples of different sizes.

Electrophoretic data were treated by various statistical methods to obtain estimates of population structure and genetic relationships within and among populations. A *G*-test for goodness of fit was used to determine whether observed genotypic values fit Hardy-Weinberg expectations. The frequent observation that triploids did not exhibit typical clonal variation patterns led to the unorthodox calculation of Hardy-Weinberg proportions following $(p + q)^3$ for a locus with two alleles. In all but two cases (*6Pgdh-1* in populations T6 and T30), loci resembled a biallelic system; the mean sums (over 11 collections) of their most common and second most common allele equaled (mean ± SE) 0.955 ± 0.058, 0.997 ± 0.004, and 0.971 ± 0.044 for *6Pgdh-1, 6Pgdh-2,* and *Mdh,* respectively.

G-contingency statistics were employed to test for allele frequency heterogeneity between ploidy levels within populations as well as across populations and areas for each ploidy level. Alleles at a locus were pooled to the nearest migrating one, when necessary, to ensure that all cells in the *G*-test had an observed number of more than 3; null alleles in triploids were lumped to the most common allele.

TABLE 2. Number of electrophoretic alleles shared by diploid and triploid *Taraxacum.* The column "shared" contains minimum estimates, because in various populations the other ploidy level was inadequately studied.

Locus	Total no. of alleles observed	No. of alleles		
		In diploids	In triploids	Shared
6Pgdh-1	8	7	6	5
6Pgdh-2	7	6	5	4
Mdh	5	4	5	4

Estimates of population structure, inbreeding, and gene flow in diploid samples were calculated by *F*-statistics (Wright 1978) according to the protocol of Weir and Cockerham (1984) with variances estimated by jackknifing over populations or loci. Corrections for unequal sample sizes can lead to slightly negative F_{ST} values; these were set to 0. F_{ST} values were tested for departure from 0 by the χ^2 method of Workman and Niswander (1970). Inbreeding coefficients (F_{IS}) were evaluated by the χ^2 test developed by Li and Horvitz (1953). F-statistics also allow for a quantitative estimation of gene flow following $F_{ST} = 1/[4N_em + 1]$, N_em being the average number of migrants exchanged between populations (Wright 1951).

RESULTS

The results are presented in two sections describing in order, the local and regional variability patterns in diploids and triploids, and the clonal composition of triploid samples.

Geographic Variation Patterns

In *Taraxacum* section *Ruderalia* diploids and triploids shared virtually all of the same major enzyme polymorphisms in both western mixed distribution area (WMA) and eastern mixed distribution area (EMA) (summarized in table 2); this similarity also applies to the other polymorphic loci that were investigated occasionally (Menken et al. 1989). Low-frequency allozymes were mostly area or population specific; in some populations, sample sizes exceeding ten were available from one ploidy level only (table 1).

In all diploid and triploid populations *d* and *g* alleles predominated at the *6Pgdh-1* locus. Allele *b* occurred at low frequencies in most western populations at both ploidy levels and in T25 from Austria where it was found in single dose in one triploid. Allele *i,* on the contrary, appeared at low frequency in all diploid and most triploid eastern populations. Furthermore, rare allele *j* was encountered in some western diploid and one eastern triploid population. Finally, four triploid samples harbored null alleles, and in T5 two asymmetrical *6Pgdh-1 dg* genotypes were found at the diploid level. In nearly all cases, *6Pgdh-1* contributed most to heterozygosity.

At the *6Pgdh-2* locus, *c* was by far the most common allele in all populations at both ploidy levels. Second most common in diploids and triploids was allele *b,* except for allele *d* in

TABLE 3. Single-locus *G*-values for among-population homogeneity in allele frequencies in diploid and triploid *Taraxacum*. Populations from the eastern and western mixed-distribution area were analyzed separately and in combination.

Locus	Area	df	*G*-value
Diploids			
6Pgdh-1	East	12	39.36***
	West	13	134.22***
	Total	40	259.75***
6Pgdh-2	East	6	13.76*
	West	13	70.59***
	Total	20	92.84***
Mdh	East	6	3.63
	West	13	26.48*
	Total	20	46.72***
Triploids			
6Pgdh-1	East	2	5.50
	West	7	51.60***
	Total	10	75.35***
6Pgdh-2	East	2	5.69
	West	7	25.94***
	Total	10	32.37***
Mdh	East	2	4.70
	West	7	89.05***
	Total	10	97.37***

* $P < 0.05$; *** $P < 0.001$.

T30 and *e* in T4 (table 8). Allele *d* also appeared in two other triploid samples and *e* in one more at frequencies of approximately 0.01. Alleles *a* and a null allele were scored once each. Allele *f* was found in four individuals in population T5.

All diploid and triploid populations contained *e* as the most common and *c* as the second most common allele at *Mdh*. Rare allele *a* occurred in quite a few populations from WMA and EMA. Occasionally null alleles were observed in triploids. Allele *d* was observed in T2 (both ploidy levels) and T20 (in diploids only).

The among-population variability in allele frequencies in WMA and total area (TA) deviated significantly from homogeneity at all three loci; among EMA populations, however, only the two *6Pgdh* loci in diploids deviated significantly from homogeneity (*G*-contingency test; table 3). *F*-statistics corroborated these heterogeneous patterns (table 4).

TABLE 5. Single-locus *G*-values for intrapopulation homogeneity in allele frequencies between diploids and triploids in nine populations of *Taraxacum*.

Population	Locus		
	6Pgdh-1	*6Pgdh-2*	*Mdh*
T2	0.81	0.51	5.26*
T6	5.34	0.01	6.53*
T10	1.06	3.28	8.28**
T11	0.11	4.22*	3.69
T19	4.01*	2.66	0.78
T20	2.53	3.13	0.38
T25	8.92**	0.96	0.04
T27	6.13*	—	1.66
T30	15.88***	3.76	3.89*

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$; df = 1 except for T6, T25, T27, and T30 at *6Pghdh-1* and T-6 at *Mdh*, which have df = 2.

Significant genetic differentiation (F_{ST} values) was observed among diploid populations for all loci with the exception of *Mdh* in EMA. In most cases, a nonsignificant excess of heterozygotes was found (negative F_{IS} values), indicating that populations simulate panmixis. In TA as well as WMA the primary component of F_{IT} was F_{ST}, whereas the F_{IS} component was rather large in EMA. This corroborates data from the majority of plant species that distribute more of their genetic variability among rather than within populations (Loveless and Hamrick 1984; Soltis and Soltis 1987). Mean gene-flow levels among diploid populations were similar in TA and WMA (N_em = 3.7 and 3.1, respectively), whereas the much smaller EMA showed a five times higher estimate of gene exchange (table 4). The inferred gene flow levels are relatively high compared with most animal-pollinated outcrossed species (e.g., Soltis and Soltis 1987).

Overall expected heterozygosity levels did not differ significantly among the three areas or between the ploidy levels (data not shown; Student *t*-test). Within each population, homogeneity between diploids and triploids in allele frequencies was observed in the majority of cases (table 5). Population T20 was uniform at all three loci and T30 heterogeneous at *6Pgdh-1* and *Mdh*, with *6Pgdh-2* bordering significance. The remaining seven populations were significantly heterogeneous at one locus. All three loci were involved in the deviations.

TABLE 4. Single-locus estimates of *F*-statistics and levels of gene flow (N_em) in diploid *Taraxacum*. Populations are organized in eastern, western, and total distribution area. Variance of mean was estimated by jackknifing across loci.

Area	Locus	F_{IS}	F_{ST}	F_{IT}	N_em
East	*6Pgdh-1*	−0.047	0.029***	−0.016	8.3
	6Pgdh-2	−0.055	0.020*	−0.033	12.1
	Mdh	−0.107	0.000	−0.122	—
Mean ± SD		−0.075 ± 0.030	0.014 ± 0.017	−0.060 ± 0.047	18.1
West	*6Pgdh-1*	−0.017	0.105***	0.089	2.1
	6Pgdh-2	0.072	0.102***	0.167	2.2
	Mdh	−0.052	0.017*	−0.034	14.2
Mean ± SD		−0.013 ± 0.024	0.075 ± 0.032	0.063 ± 0.049	3.1
Total	*6Pgdh-1*	−0.028	0.090***	0.065	2.5
	6Pgdh-2	0.049	0.096***	0.140	2.3
	Mdh	−0.075*	0.017*	−0.057	14.5
Mean ± SD		−0.035 ± 0.024	0.064 ± 0.030	0.031 ± 0.052	3.7

* $P < 0.05$; *** $P < 0.001$.

TABLE 6. Single-locus *G*-tests for deviation from Hardy-Weinberg equilibrium in eight populations of triploid *Taraxacum*.

Population	Locus		
	6Pgdh-1	*6Pgdh-2*	*Mdh*
T6	7.78**	0.16	0.64
T10	0.48	0.12	0.28
T11	8.60**	0.07	22.86***
T19	0.21	0.32	0.01
T25	0.40	0.08	0.70
T30	14.27***	8.27**	0.06
TCB	0.09	0.26	0.11
TCC	0.12	0.17	0.00

** $P < 0.005$; *** $P < 0.001$ (df = 1).

All diploid populations had genotypic distributions not significantly deviating from Hardy-Weinberg proportions (data not shown; see F_{IS} values in table 4). Surprisingly, a majority of the triploid samples also appeared to conform to a Hardy-Weinberg equilibrium (table 6). Of 24 comparisons in eight populations (only samples exceeding 20 individuals were used) only five cases from three populations differed from Hardy-Weinberg expectations (under total outcrossing, one is expected from type I errors; $\chi^2 = 12.7$, df = 1, $P < 0.01$). There was no clear pattern to these deviations though: cases that showed significant deviations involved all three loci, and three of the cases exhibited a heterozygote excess, two a deficit. The three populations showing deviations from Hardy-Weinberg proportions were the very ones that exhibited the most intrapopulational heterogeneity in allele frequencies between the ploidy levels (table 5), viz., T6 (*Mdh* heterogeneous and *6Pgdh-1* bordering significance), T11 (*6Pgdh-2* heterogeneous and *Mdh* bordering significance), and T30 (*6Pgdh-1* and *Mdh* significantly differing from homogeneity and *6Pgdh-2* bordering significance).

Clonal Composition of Triploid Samples

All 11 triploid population samples were multiclonal (tables 7, 8). The number of clones detected per population ranged from 6 to 17 with a mean ± SE of 11.8 ± 3.6 (weighted mean 13.1). Among 374 individuals, 57 clones were encountered, 63.2% of which were restricted to one population (so-called private clones), and 49.1% (i.e., 77.8% of 63.2%) were represented by a single individual (unique clone). The mean number of populations (± SE) containing a particular clone was 2.3 ± 2.2. The number of widespread clones (defined as those present in more than 70%, that is, eight or more, of the population samples) was only three; clone 25 occurred in all but one (T27) populations and clones 34 and 19 in eight populations. Consequently, populations showed intermediate levels of evenness (range 0.26–0.85 with a mean ± SE of 0.54 ± 0.18), indicating that populations were seldom dominated by a single genotype (such as clone 33 in T11 with a frequency of 0.509; population evenness, 0.26) or composed of numerous clones in similar frequencies (like in population T30; evenness, 0.85). These patterns of localized distribution concur largely with other clonal species (Ellstrand and Roose 1987).

The number of characters (loci) scored and the number of genotypes detected were correlated (Kendall's $\tau = 1.00$, $P < 0.05$), as were sample size and number of genotypes ($\tau = 0.574$, $P < 0.01$), but not sample size and genotypic diversity ($\tau = 0.055$, NS). Actually, H_g was very constant among collections ranging from 0.709 to 0.886 with a mean ± SE of 0.820 ± 0.055 (table 7). Viewed separately, *6Pgdh-1, 6Pgdh-2,* and *Mdh* had a similar resolution detecting 11, 9, and 10 clones, respectively. Combinations of two loci revealed an average 29.3 ± 4.2 clones (2.93 factor of increase), whereas all three loci together described 57 clones (factor 1.94).

DISCUSSION

Clonal Diversity

Sampling Intensity.—The data presented are conservative estimates of genic variability, because sampling intensity was low. Apart from the inability of the zymogram technique to detect all variation (allozyme bands effectively are electromorphs, that is, collections of similarly charged enzyme molecules that differ in their amino-acid sequence at one site at least; King and Ohta 1975), a given *Taraxacum* genotype may comprise a heterogeneous collection of individuals sharing an identical three-locus electrophoretic profile. Null alleles (through gene silencing) are particularly difficult to detect. Because our electrophoretic procedures are mainly qual-

TABLE 7. Summary of clonal diversity estimates of 11 triploid *Taraxacum* populations. Populations originate from western (T2-TCC) and eastern distribution areas (T19-T27). Number in parentheses below population name is the sample size.

	Population										
	T2 (14)	T6 (24)	T10 (36)	T11 (53)	T20 (15)	T30 (30)	TCB (45)	TCC (79)	T19 (29)	T25 (38)	T27 (11)
No. of clones	7	12	11	13	8	16	12	15	13	17	6
Effective no. of clones*	4.7	8.2	6.1	3.4	6.8	8.3	4.5	5.7	5.5	8.8	4.5
Proportion distinguishable†	0.5	0.5	0.31	0.24	0.53	0.53	0.27	0.19	0.45	0.45	0.55
No. of private clones‡	1	4	3	2	2	10	3	4	2	5	0
No. of unique clones§	4	7	4	5	3	11	7	7	9	11	3
Clonal diversity‖	0.786	0.878	0.836	0.709	0.853	0.88	0.778	0.824	0.818	0.886	0.776
Clonal equitability (evenness)#	0.67	0.68	0.55	0.26	0.42	0.85	0.52	0.75	0.52	0.37	0.38

* Calculated as $1/\Sigma\, p_i^2$, p_i being the frequency of the ith clone.
† Number of clones divided by sample size.
‡ A private clone is restricted to one population.
§ A unique clone is represented by one individual.
‖ Calculated as $1 - \Sigma\, p_i^2$, p_i being the frequency of the ith clone.
Effective number of clones divided by number of clones.

TABLE 8. Examples of genotypic composition and frequencies of diploids and triploids in mixed *Taraxacum* populations. Genotypes are described in the order *6Pgdh-1-6Pgdh-2-Mdh*. Numbers in parentheses after the ploidy level indicate sample size.

Population T4		Population T10		Population T19		Population T30	
Triploids (7)	Diploids (46)	Triploids (36)	Diploids (42)	Triploids (29)	Diploids (35)	Triploids (30)	Diploids (35)
ddd-ccc-eee 0.143	dd-cc-ee 0.196	bdd-bcc-eee 0.028	bg-bc-cc 0.024	ddd-bbc-cce 0.034	dd-bc-ce 0.028	bdg-cdd-eee 0.033	dd-cc-ce 0.057
ddg-ccc-eee 0.286	dd-ce-ee 0.022	bdd-ccc-cee 0.055	bg-bc-ee 0.024	ddd-bbc-cee 0.034	dd-bc-ee 0.029	bdd-ccc-cee 0.033	dd-cc-ee 0.086
ddg-cce-eee 0.286	dd-ee-ce 0.022	ddd-bbb-eee 0.028	bg-cc-ce 0.024	ddd-bcc-cce 0.034	dd-cc-cc 0.028	ddd-ddd-eee 0.033	dd-cd-ee 0.057
dgg-cce-cee 0.143	dg-cc-ce 0.043	ddd-bcc-eee 0.028	dd-bb-ce 0.024	ddd-bcc-cee 0.069	dd-cc-ce 0.257	ddd-bcc-eee 0.033	dg-cc-ce 0.028
ggg-cce-eee 0.143	dg-cc-ee 0.348	ddd-ccc-eee 0.083	dd-bc-ee 0.071	ddd-bcc-eee 0.034	dd-cc-ee 0.229	ddd-ccc-eee 0.133	dg-cc-ee 0.200
	dg-ce-ce 0.043	ddg-bbc-eee 0.056	dd-cc-ce 0.167	ddd-ccc-cee 0.207	dg-cc-ce 0.171	ddd-ccd-cce 0.033	dg-cd-ce 0.086
	dg-ce-ee 0.065	ddg-bcc-cee 0.055	dd-cc-ee 0.167	ddd-ccc-eee 0.345	dg-cc-ee 0.200	ddg-ccc-eee 0.033	dg-cd-ee 0.086
	dg-ee-ce 0.043	ddg-bcc-eee 0.028	dg-cc-cc 0.048	ddg-ccc-cce 0.034	di-cc-ce 0.057	dgg-ccc-eee 0.033	dg-dd-ce 0.057
	dg-ee-ee 0.022	ddg-ccc-eee 0.250	dg-cc-ce 0.214	ddg-ccc-cee 0.069		dgg-ccd-eee 0.067	dg-dd-ee 0.086
	gg-cc-ee 0.087	dgg-bcc-cee 0.250	dg-cc-ee 0.190	ddg-ccc-eee 0.034		ggg-ccc-cce 0.067	gg-cc-ee 0.114
	gg-ce-cc 0.022	dgg-ccc-eee 0.139	gg-bc-ee 0.024	dgg-ccc-cee 0.034		ggg-ccc-eee 0.033	gg-cd-ce 0.029
	gg-ce-ce 0.022		gg-cc-ee 0.024	dgg-ccc-eee 0.034		bgg-ccc-cce 0.033	gg-cd-ee 0.086
	gg-ce-ee 0.043			ddi-ccc-cee 0.034		bgg-ccc-cee 0.267	gg-dd-ce 0.028
	gj-cc-ee 0.022					bgg-ccd-ace 0.033	
						bgg-cdd-oce 0.033	
						bgg-cdd-cee 0.100	

itative, triploids scored as homozygotes might be heterozygotes with one or even two null alleles. The oldest clone should exhibit the greatest gene silencing. Assuming the age of a clone can be based on being most abundant and/or widespread, then clone 25 is the oldest; it is homozygous at all three loci, indeed. Undoubtedly, this "clone" in particular is a heterogeneous collection of genotypes.

Taraxacum section *Ruderalia* is no exception to the rule that a strong correlation exists between the number of characters used for genotyping and the number of clones detected (Ellstrand and Roose 1987). The discriminatory power of an added locus depends heavily on its overall heterozygosity and number of alleles. There is also a saturation effect when increase in diversity per added locus becomes negligable as single individual clones cannot be differentiated by applying more characters for genotyping. In some of our samples, a fourth locus was studied for increasing the resolution of genotyping (viz., alcohol dehydrogenase, shikimate dehydrogenase, phosphoglucomutase, or leucine aminopeptidase; data not shown). The average increase was 1.63 ± 0.40, leading to the discovery of 93 clones. This is an underestimate because not all individuals could be scored at a fourth locus, and the dosage effect in monomers (all but alcohol dehydrogenase) does not always allow for correctly genotyping of both triploid heterozygotes at such loci. In an unpublished study, we found within a single population 72 clones among 263 individuals genotyped at five polymorphic loci; this figure fits very well on the regression line based on the present information over four loci. After extrapolation, one arrives at some 16 polymorphic loci required to tell all individuals genetically apart.

Allozyme studies show that multiclonal species vary in the extent of clonal diversity. Technically, this can be explained by differences in sampling and sample size, and the number of loci (and their variability levels) used for genotyping. Data from the literature (summarized in table 2 of Ellstrand and Roose 1987) allow a comparison between our results and eight clonal species for which genotyping relied exclusively on information from enzymes for which the genetic basis is known. Except for *Populus tremuloides,* where every individual differs for a 26-locus profile, all species have a low clonal diversity. The average proportion distinguishable, a good overall means of describing diversity, is 0.16 ± 0.34 (or 0.04 ± 0.04 if *P. tremuloides* is excluded) with genotyping based on between 10 and 26 loci (mean 17.1 ± 5.1) compared with 0.41 ± 0.13 based upon as few as three loci in *Taraxacum.* The average of 17 loci would probably have been sufficient to tell every *Taraxacum* individual apart.

Taraxacum has a high clonal diversity indeed. This wealth of diversity is also evident at the molecular level, in which variability seems to be higher than in many other plant species (King and Schaal 1990; King 1993). The high level of variability in *Taraxacum* section *Ruderalia* might facilitate adaptive evolution and account for its successful invasion of man-disturbed habitats.

Evolutionary Factors.—Apart from differing data sets, species might actually vary in clonal diversity because of differences in their mode of transition to asexuality (monophyletic versus polyphyletic), in time since this transition (assuming a molecular clock), in population genetical factors

(e.g., bottlenecks, drift, migration, and replacement of inferior genotypes), and in ecological width (generalists versus specialists). The difficulty of assessing the relative contributions of such factors, due to lack of powerful quantitative analytical methods (Hebert et al. 1988), means that it is hard to choose among various explanations, but some remarks can still be made.

Broadly speaking, a strict monophyletic origin results in one predominant clone with (a number of) satellite clones, that are related to one another by single mutational steps (for instance, *T. hollandicum,* section *Palustria;* Battjes et al. 1992). A polyphyletic origin results primarily in a number of common clones that possibly differ from one another at a number of loci and rare clones around every common clone from mutational input. Changes will subsequently occur owing to differing population genetical factors. Carried to extremes, the pattern and level of clonal variability could evolve to similarity if (1) a monophyletic species produces through mutation some highly competitive general purpose clones, whereas intermediate genotypes [one mutational step clones] are eliminated by selection, (2) clonal diversity in a polyphyletic species is drastically reduced after a severe bottleneck or by means of natural selection leaving one well-adapted clone with some satellites, and (3) gene silencing weeds out divergent alleles and leaves the common ones. Below we argue that the large clonal diversity of triploid *Ruderalia* is most simply explained by an ongoing polyphyletic origin with probably an additional effect of a high mutation rate (see also King 1993).

Gene Flow between Ploidy Levels

Inferred Population Genetical Evidence.—Strict apomicts evolve separately along clonal lines. However, when bidirectional hybridization takes place between diploids and triploids a different picture appears: mutations arising in one ploidy level will appear in the other after some time, and consequently, variation patterns will be highly similar. This is exactly what has been found in the present study: diploids and triploids share all major and most minor polymorphisms. Comparable patterns were observed by Hughes and Richards (1988).

The average frequency of private alleles (i.e., alleles that occur in one population only) are indicative of levels of gene flow (in terms of diploid individuals) between populations (Slatkin 1985). Similarly, alleles in triploids that do not show up in diploids of that same population or *vice versa* might be suggestive of separately evolving units. Actually, no more than five alleles unique to one population were encountered. Within that population, the private alleles were restricted to one ploidy level, four of them occurred in diploids and one in triploids; unfortunately, in most cases fewer than ten individuals from the other ploidy level were analyzed. Their absence can thus easily be explained by sampling error.

The near dearth of alleles unique to the parthenogens adds to the gene-flow hypothesis, the more so because apomictic *Taraxacum* probably generate appreciable amounts of genetic variation by nonmeiotic processes (Richards 1989; King and Schaal 1990). Two null alleles present in three and four populations, respectively, were restricted to the triploid component with frequencies ranging from 0.004 to 0.015. Sampling error can again account for the absence of these rare alleles from the other ploidy level. Moreover, null alleles are less easily detected in field samples of diploid sexuals, because heterozygotes for null alleles will be scored as homozygotes for the other allele. However, this would cause heterozygote deficiencies, whereas heterozygote excess was detected (table 4; generally negative F_{IS} values). Alternatively, the absence could be real because null alleles that encode essential proteins will be selected against more effectively in sexuals than in triploid asexuals.

As for the diploid component, the average frequency of private alleles was a low 0.021 ± 0.007. The gene flow estimate calculated from the average frequency of private alleles ($N_em = 5.8$, when adjusted for sample size; Slatkin 1985) is similar to the one based on inbreeding coefficients ($N_em = 3.7$, table 4). This means that nearby populations might reach appreciable levels of gene exchange. We assume triploid pollen grains and seeds to behave in a manner similar to that of the diploids.

A clear indication of intrapopulational pollen flow between ploidy levels comes from two alleles (viz., *6Pgdh-2-d* in T30 and *6Pgdh-2-e* in T4; table 8) that were almost restricted to a single population but that occurred at both ploidy levels in considerable frequencies. The other populations in which these two alleles occur are situated at large distances and achieve only very low frequencies; homology of alleles, therefore, might be questioned.

Asexual reproduction leads to very great linkage disequilibrium; of all possible genotypes only a few are usually realized and furthermore, many loci will show large deviations from Hardy-Weinberg proportions. This picture only partially matches with the situation observed in *Taraxacum* section *Ruderalia.* In about 80% of the triploid cases, were the three study loci in Hardy-Weinberg equilibrium (table 6). Yet, there is ample evidence for apomixis, because some populations clearly showed deviations from Hardy-Weinberg expectations in addition to linkage disequilibria typical for an asexual, fixed genetic profile (the three study loci are not linked; Menken et al. 1989); linkage disequilibria were not calculated due to generally low numbers per genotypic class. In T30, for instance, allele *6Pgdh-1-b* is lacking in diploids whereas it occurs at the triploid level in 16 out of 30 individuals and 7 of 16 clones; none of five *6Pgdh-1-bgg* clones in 14 individuals, however, have *eee* genotypes at *Mdh,* whereas 12 other triploid individuals spread over 8 clones do show *Mdh-eee* genotypes (table 8). The possibly low level of gene exchange between ploidy levels is also reflected in this population that displays the least homogeneous relationship between ploidy levels (table 5) and together with T11 shows the most deviations from Hardy-Weinberg equilibrium (table 6). Most likely, allele *6Pgdh-1-b* arose in a triploid individual and pollen flow was absent or took place chiefly or exclusively from diploids to triploids. As mentioned before, the shared but private allele *6Pgdh-2-d,* which is rather randomly distributed over seven clones in single, double, or triple dose, supports the idea of pollen flow from diploids to triploids in this very same population. Therefore, it is likely that both apomixis and hybridization between diploids and triploids operate in mixed natural populations of *Taraxacum*

section *Ruderalia,* though the amount of each cannot be estimated from our data.

Under the assumption of pollen flow between diploids and triploids, clonal diversity is expected to be lower in completely apomictic areas than in mixed ones. Over the last two or three centuries, *Taraxacum* section *Ruderalia* were introduced into the United States, but sexual individuals have never been observed (King 1993 and references therein). After allozyme analysis at five loci, Lyman and Ellstrand (1984) indeed found a much lower incidence of clonal diversity than our estimates: 21 different clones among 518 individuals from 22 populations. They explained this in comparison with other apomicts—there is, nevertheless, a large amount of variability caused by multiple introductions—but did not rule out that somatic mutations may also play an important role. The role of mutations within asexual lineages was established by King and Schaal (1990). A combined nuclear and chloroplast DNA analysis of North American and European dandelions, however, showed that multiple hybridization has been a more important source of genotypic variation than mutation (King 1993). Before King's studies, large numbers of new variants were observed in progenies of apomictic plants both in chromosomal constitution and at some enzyme loci (Richards 1986; Mogie and Ford 1988). We do not have data from Northern European populations that are entirely obligately apomictic. However, a latitudinal trend in clonal diversity (a decrease towards increasingly triploid regions; fig. 1) has not been observed: genotypic diversity was very constant among collections with a mean ± SE of 0.820 ± 0.055 (table 7).

Furthermore, the northern-most collections TCB and TCC were almost entirely triploid but harbored many clones and were in Hardy-Weinberg equilibrium at all three study loci (table 6). Gene flow (i.e., pollen flow and/or seed movement) from neighboring areas can explain these patterns, as diploid/triploid ratios in this area change quickly over short distances, and our N_em values for diploids suggest considerable amounts of gene flow over such distances. Population TB1, for instance, with some 50% diploids was sampled in a pasture adjacent to TCB and TCC (Elzinga et al. 1987). Finally, triploid populations entirely in Hardy-Weinberg equilibrium, suggestive of a high level of gene exchange, did not have more clonal variation as measured by the effective number of clones than those that had one or more loci deviating (Student t-test).

Actual Processes.—All that has been presented so far on gene exchange was inferred from population genetical data. Actual documentation of hybridization in the field comes from a multitude of processes observed in greenhouse and field experiments that could cause bidirectional gene flow between diploids and triploids under natural conditions (for an overview of these processes and for references see the introduction). In a nutshell, these comprise unreduced gametes in diploids, reductional euhaploid pollen from obligate and facultative agamosperms, and haploid eggs from the latter.

The discovery of a complex mixture of diploid, triploid, tetraploid as well as aneuploid individuals in the progeny of single sexuals that were experimentally introduced into entirely asexual populations established the occurrence of pollen flow from triploids to diploids (Sterk 1987). Extension to crosses in which transmission of pollen alleles was investigated electrophoretically, however, produced a different picture. In experimental crosses between sexual *Mongolica* mothers and asexual *Ruderalia* fathers, an average 85% of the progeny resulted from self-fertilization, whereas only 3% selfing was observed in sexual crosses between *Mongolica* parents using the same mother plants (Morita et al. 1990). Similarly, in crosses between diploid *Ruderalia* and triploid apomictic *Taraxacum pseudohamatum,* less than 15% of the claimed hybrids (Hughes and Richards 1988) could actually be allozymically confirmed as such (Morita et al. 1990). Even some progeny from sexual crosses within the section *Ruderalia* could be better explained by selfing (Menken et al. 1989). If under natural conditions triploid *Ruderalia* pollen has the same effect of inducing self-fertilization in diploid *Ruderalia* as it has on diploid *Mongolica,* then much inbreeding is to be expected. This is clearly not in accord with our findings of general, albeit small heterozygote excesses in diploids (table 4). More specifically, in the three populations in which diploids are likely to receive much triploid pollen (30% or less diploids; viz., T2, T11, and T30), heterozygote deficit was observed in only one out of nine cases, all others showing an excess. It is possible though, that seedlings derived from selfing quickly disappear from the population; Morita et al. (1990) observed inbreeding depression in selfers even in the mild environment of the greenhouse. Alternatively, either the self-incompatibility system of *Ruderalia* is more stringent or the *Mongolica* results in the glasshouse are merely an artifact of some sort.

The amount of genotypic variability in triploids might further support the pollen-flow hypothesis. Almost every second clone is unique, a level of variability approaching that of an amphimictic species, the more so if the limited sampling intensity is considered. Theoretically, polyploids have the capacity to store more genetic variation than do diploids, certainly so if they are amphimicts. Indeed, in 21 of 26 comparisons, triploid *Ruderalia* had higher heterozygote percentages and exhibited a generally higher number of genotypes per population than diploids (corrected for sample size; some examples are given in table 8), but they realize less of the theoretically possible genotypic combinations. Due to the probably high mutation rate of *Taraxacum,* high diversity is not necessarily proof of gene exchange. However, under the assumption of separate evolution of the two ploidy components, unusually high mutation rates to electrophoretically identical alleles must be invoked to explain the observed intrapopulational homogeneity between the ploidy levels.

There are two other processes that could lead to the observed genetic homogeneity. First, the repeated origin at high frequency of triploids from diploid matings, a process that has been used to explain the high frequency and genetic uniqueness of triploid fern clones (Haufler et al. 1985); the existence of polyploidy is generally considered to be proof of the occurrence of unreduced gametes. The probability of such a polyphyletic origin of asexuals depends on how often unreduced gametes are being produced in diploids. Sexual crosses, performed over the past 10 yr, within and between the sections *Ruderalia* and *Mongolica* produced sexual, incompatible diploids without exception (Jenniskens 1984;

Menken et al. 1989; Morita et al. 1990; unpubl. results). The occurrence of unreduced gametes in diploids, therefore, is supposedly rare.

Second, new triploids could arise from haploid pollen, originating from sexuals or asexuals, fertilizing diploid eggs of facultative agamosperms. We do not have estimates of actual frequencies in nature of facultative apomixis but gathered some genetic evidence from experimental crosses. In *Taraxacum* section *Ruderalia* crosses between *Mdh eee* × *cc,* of 138 offspring, 3 were *cee,* 1 *ce,* and the remainder *eee* (or *ee,* as we did for *Mdh,* not study this electrophoretic phenotype cytologically). Unfortunately, the breeding systems of these F_1 plants were not checked. At any rate, paternal alleles were transmitted to an obviously facultative agamosperm. Together with a substantial rate of new mutations these two processes could explain the large amount of clonal diversity in triploids.

The common occurrence of diploids in western Europe makes it very likely that diploid seeds have reached North America in the past 250 yr. However, the absence from this region of sexual diploids (King 1993 and references therein) could be indicative of the adaptive differences between the cytotypes. The ecological amplitude of diploid plant species is usually more restricted than that of closely related polyploid taxa (see introduction). Strong selection pressures (*Taraxacum* commonly occurs on roadsides in North America) can thus account for the absence of diploids. Selection together with founder effects and the impossibility to exchange genes with diploids might explain the relative dearth of clonal diversity in North America in comparison with western and central Europe.

Conclusions

In summary, we found substantial evidence for extensive exchange of genetic material between diploids and triploids within local populations of *Taraxacum* section *Ruderalia.* This evidence, such as the sharing of all major and most minor polymorphisms, the virtual absence of ploidy level-specific alleles, the intrapopulational homogeneity in allele frequencies between ploidy levels, and Hardy-Weinberg equilibrium in triploids give weight to the pollen flow hypothesis, along with the direct evidence from experimentally observed gene exchange mechanisms. Asexuality is advantageous in preserving genotypes well-adapted to the immediate environment, whereas sexual recombination provides the variation necessary for adaptation and long-term evolution. *Taraxacum* section *Ruderalia* seems to combine the advantages of these two different breeding systems, the sexual component of which includes primarily cross- but also self-fertilization. The recurrent recruitment of clones from sexuals, from hybridization between sexuals and asexuals, and from mutation pressure is likely to account for the high genetic and ecological diversity of the asexual component of *Taraxacum* section *Ruderalia.* Not only may clonal diversity be replenished constantly by the formation of new asexual genotypes, pollen flow also guarantees new genetical input into the diploids. Parallel selection for shared alleles in similar environments might add to the similarity of distribution of genic variability in the two ploidy levels.

There may be (genetic) variation in pattern and intensity of pollen flow. Differences among populations in (1) homogeneity in allele frequencies between ploidy levels and (2) the extent to which triploid populations simulate Hardy-Weinberg equilibrium combined with (3) typical patterns of clonal diversity suggest that the relative contributions of pollen flow and apomixis on population variability probably differ by locality.

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