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Morphometric studies of the *Euphorbia esula* group in North America[1]

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Leafy spurge and cypress spurge are important weeds of pastures and unimproved rangeland in western and eastern North America, respectively. Taxonomists disagree as to whether leafy spurge is a single variable species or an aggregate of two or more species. Morphometric techniques (clustering by incremental sum of squares and principal coordinate analysis) were used to analyze relationships in leafy spurge and its allies. On the basis of studying 26 morphological characters found in 200 collections representing 32 putative taxa, we concluded that in North America only four species should be recognized, namely, *Euphorbia agraria* Bieb., *Euphorbia cyparissias* L., *Euphorbia esula* L., and *Euphorbia* × *pseudoesula* Schur. A key to these taxa is provided. No authentic material of *Euphorbia lucida* Waldst. & Kitt. and *Euphorbia salicifolia* Host was found from this continent in the collections we examined.

Introduction

Leafy spurge, *Euphorbia esula* L., is a native of Europe and temperate Asia (Smith and Tutin 1968; Radcliffe-Smith 1985). It was introduced to coastal Massachusetts in the early 1800s, perhaps in ballast (Britton 1921). It was introduced separately into western North America, probably as a contaminant of seed brought by Mennonites emigrating from southern Russia (Dunn 1985). A closely related species, cypress spurge (*Euphorbia cyparissias* L.) is a weed of pastures, roadsides and limestone escarpments, particularly in eastern North America. Cypress spurge also first appeared on this continent in the 19th century. A sterile diploid form was used as an ornamental in cemeteries from whence it escaped. Later, a fertile tetraploid form was introduced accidentally in contaminated grass seed (Stahevitch *et al*. 1988*a*).

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Leafy spurge, cypress spurge, and their allies belong to section *Esula* Prokh. of subgenus *Esula* (Roeper) Koch in the Euphorbiaceae. There is considerable disagreement among botanists as to whether leafy spurge is a single variable species or a complex of species (sometimes referred to as the *Euphorbia esula* or the *Euphorbia virgata* aggregate). Cypress spurge is reported to form hybrids with leafy spurge, and it has been suggested that the two taxa share one or more genomes (Pritchard 11958, 1960). The taxonomic issue is not of mere academic interest. Leafy spurge and cypress spurge (particularly the 4*x* cytotype) are serious weeds of pastures and roadsides in western and eastern North America (Rousseau 1968; Dunn 1979; Best *et al*. 1980; Ebke and McCarty 1983; Frankton and Mulligan 1987). Leafy spurge can reduce the livestock carrying capacity of pasture between 50 and 75%. Furthermore, both leafy and cypress spurge contain a highly caustic latex that produces scours and occasionally causes death in cattle (Lym and Kirby 1987). Several closely related spurge taxa are also adventives, but these occur only sporadically and have not yet become serious weeds. Occasionally, they have been confused with true leafy spurge. Leafy and cypress spurge are the targets of a number of large biological control programs in both Canada and the United States, whose success may be partly dependent on a correct interpretation of spurge taxonomy (Harris 1984; Watson 1985).

Review of the taxonomic literature

Linnaeus (1753) described five species of spurge belonging to what we now recognize as section *Esula* of subgenus *Esula*, including the two of particular concern to us, namely *E. esula* and *E. cyparissias*. Later, Waldstein and Kitaibel (1804) described two additional ones, *Euphorbia virgata* and *Euphorbia lucida*. Boissier (1862) included 22 species in his treatment. He considered both *E. esula* L. and *E. virgata* Waldst. et Kit. to be polymorphic taxa, which he divided into several intraspecific forms (e.g., *E. virgata uralensis* and *E. virgata orientalis*). Other authors (Fischer 1822; Croizat 1945; Prokhanov 1949) treated these as full-fledged species. Zimmerman (1924) and Soo (1925, 1930, 1980) considered the leafy spurge aggregate to be comprised of six taxa (although they did not agree on which six). Schur (1866) recognized 9, Klokov (1955) 12, Prodan (1953) 14, and Prokhanov (1949) 34. In their treatment of *Euphorbia* for "Flora Europaea," Smith and Tutin (1968) assigned 11 species to section *Esula*. They considered leafy spurge to be a single species (*E. esula*), which they divided into two subspecies: (i) ssp. *esula* comprises *Euphorbia borodinii* Sambuck, *Euphorbia filicina* Portenschl., *Euphorbia imperfoliata* Viz., *Euphorbia pancicii* Beck, and *Euphorbia pseudoagraria* Smirnov; (*ii*) ssp. *tommasiniana* Bertol. comprises *Euphorbia virgata*, *Euphorbia subcordata* Ledeb., *Euphorbia tenuifolia* Lam., and *Euphorbia uralensis* Fisch. ex Link.

The taxonomic problem in the leafy spurge group is supposedly further complicated by widespread hybridization. The earliest reference to hybrids appears to be Schur (1858), who describes a number of intermediates either as full-fledges species (e.g., *Euphorbia × pseudoesula, Euphorbia × pseudolucida, Euphorbia × esula-cyparissias*) or as subspecies (e.g., *E. virgata* ssp. *pseudovirgata*). Zimmermann (1924) suggested that several hybrids occur in Central Europe, including *E. cyparissias × E. esula, E. esula × Euphorbia × paradoxa* (Schur) Podp., *E. esula × E. lucida* Waldst. et Kitt., and *E. esula × E.*

virgata. Later, Soo (1925, 1930) described *Euphorbia* × *wagneri*, the putative *E. esula* × *E. lucida* hybrid, and *Euphorbia* × *gayeri* Boros & Soo, the putative *E. cyparissias* × *E. virgata* hybrid. He considered Schur's *E. virgata pseudovirgata* to be a hybrid between *E. esula* and *E. virgata*, which he names *Euphorbia* × *pseudovirgata* (Schur) Soo rather than a subspecies of *E. virgata*. Prodan (1953) included several hybrids in his account of the *Esula* group for the Romanian flora: *Euphorbia* × *pseudoesula* Schur, *Euphorbia* × *pseudolucida* Schur (*E. lucida* × *E. virgata*), *E.* × *pseudovirgata,* and *E.* × *wagneri* Soo.

For the most part, North American treatments have been more conservative than the European ones. Groh (1935), who probably was the first to address the problem, concluded that all the North American material examined by him belonged to *E. esula*.

Morton (1937) reevaluated the same material, utilizing Ostenfeld's (1903) study of leafy spurge in Denmark, and concluded that two groups of plants could be distinguished: those in which the leaves were broadest above the midpoint (which Morton designated *E. esula* s.str.), and those whose leaves were broadest at or below the midpoint (designated *E. virgata*). Like Groh, Bakke (1936), Fernald (1950), Hitchcock *et al*. (1961), and Packer (1983) considered the weedy leafy spurge to be a single species. In the most recent worldwide treatment of *Euphorbia*, Webster (1967) also considered *E. esula* to be one species. Moore (1958) tended toward Morton's view of there being two species. Croizat (1945) recognized three taxa, namely *E. virgata*, *Euphorbia* × *intercedens* Podp. (= *E.* × *pseudolucida*), and *E. uralensis*; he excluded *E. esula* sensu Morton (1937) from this continent. He also reported that three other members of the *Esula aggregate*, *Euphorbia agraria* Bieb., *E. lucida*, and *E. cyparissias*, were adventive and suggested that several others might be yet detected. Boivin (1967), in his "Flora of the Prairie Provinces" and in an unpublished manuscript, evaluated the characters which Croizat had used to segregate *E. virgata* and *E.* × *intercedens* from *E. esula*. He concluded that such splitting was unrealistic and placed the first two taxa in synonymy with *E. esula*, as had been done earlier by Hitchcock *et al*. (1961). Boivin incorrectly considered *E. lucida* and *E. agraria* to be synonymous. The most recent treatments are by Dunn and Radcliffe-Smith (1982) and Radcliffe-Smith (1985). The first considers North American populations of *E. esula* s.l. to represent five species, namely *E. esula*, *Euphorbia androsaemifolia* Willd., *Euphorbia boissieriana* (Woron.) Prokh., *E. uralensis*, and *E.* × *pseudovirgata*.

The second treatment deals with 79 species and hybrids (covering 117 names) constituting the leafy spurge aggregate (section *Esula*). Of these, 15 are reported to be definitely present in North America. Leafy spurge proper is considered to be represented in North America by 11 variants, namely *E. androsaemifolia*, *E. androsaemifolia* × *E. esula*, *E. boissieriana*, *E. boissieriana* × *esula*, *E. esula* s.str., *E.* × *gayeri, E.* × *pseudolucida, E.* × *pseudovirgata, E. uralensis, E.* × *wagneri, and E. virgata* (as *Euphorbia waldsteinii* (Sojak) Radcliffe-Smith). Four distinct but related taxa are reported to occur, namely *E. agraria, E. cyparissias, E. lucida*, and *E.* × *pseudoesula*. Several others are considered as likely to be present. This treatment is a major turnabout from Radcliffe-Smith's earliest one (Smith and Tutin 1968) in which leafy spurge was considered a single species throughout all of Eurasia. With the exception of Radcliffe-Smith (1985) and Croizat (1945), taxonomists dealing with North American spurges have recognized only one hybrid, with afore-named *E.* × *pseudoesula*.

It should be evident that most treatments of leafy spurge are found in floras. Croizat (1945) provided an extremely perceptive and entertaining discussion of the national rivalries that contributed to the enormous floristic synonymy with which this group of plants is burdened in the European literature. There have been only two systematic studies of the group. Moore (1958) carried out chromosome number determinations and synthesized hybrids between *E. esula* ($2n = 6x = 60$) and *E. cyparissias* ($2n = 2x$, $4x = 20, 40$). Attempts to produce diploid-hexaploid crosses were unsuccessful. Moore concluded that his synthetic pentaploid hybrids ($2n = 5x = 50$) were morphologically indistinguishable from the $5x$ variants occasionally encountered in central Canada as well as from the taxon described from central Europe by Schur (1866) under the binomial "*E.* × *pseudoesula*." Pritchard (1958, 1961) carried out a biosystematic study of leafy spurge in Britain and concluded that it is a single, though quite variable, species.

Radcliffe-Smith's (1985) treatment was used (in manuscript form) by Ebke and McCarty (1983) to sort 38 nursery populations of leafy spurge mostly of North American origin. They concluded that 5 of the 21 taxa identified by Radcliffe-Smith were represented by the variation in their sample, namely *E. agraria, E. cyparissias, E. esula*, and *E. uralensis*. The majority of the samples could be assigned to *E.* × *pseudovirgata*. The Ebke and McCarty study was primarily concerned with identification and was not intended to test which taxonomy best reflects the type of variation actually found in leafy spurge.

Our leafy spurge collections at DAO (herbarium acronyms as in Holmgren *et al*. 1981) include a large number of specimens or duplicates of specimens which had been examined and annotated by H. Groh, L. Croizat, R. J. Moore, and A. Radcliffe-Smith for their studies. This material (supplemented by additional European and North American collections) formed the core study material for a morphometric analysis. The results, together with those of a complementary cytogenetic study (Stahevitch *et al*. 1988*b*), should permit us to better assess the different approaches to leafy spurge taxonomy and so perhaps improve the chances for its biological control.

Materials and methods

Herbarium specimens of taxa belonging to section *Esula* were examined from the following herbaria: CAN, DAO, HUH, MG, MPU, MT, MTMG, MW, TRT, U, and W (acronyms according to Holmgren *et al*. 1981). Specimens also were supplied by P. Harris, K. Mortensen, D. Schroeder, and G. Wheeler. In all, approximately 600 specimens were examined, of which 200 representative ones (see Appendix) were selected for morphometric analyses. An attempt was made in our study to utilize taxa referred to by Radcliffe-Smith (1985) in his recent survey of the leafy spurge group. A large sample of the material annotated by him is available at DAO, representatives of which are illustrated in Figs. 1-14 in his treatment.

Since many diagnostic features in leafy spurge and its allies are associated with leaf characters, photographs of specimens can provide considerable information on various authors' species circumscriptions. Photographs of F. A. von Waldstein and P. Kitaibel's collections of *E. virgata* and *E. lucida* were obtained from BP, of Linneaen specimens of

E. esula and *E. cyparissias* from LINN, and of P.A. Smirnov's material from MW. All photographs are deposited in the DAO photographic collection of types and historical specimens.

Morphometric analyses were carried out on two sets of data. One set consisted of 200 OTUs (operational taxonomical units) representing 28 taxa and their putative hybrids collected from Europe and North America. The European material included specimens of several species that were not treated in Radcliffe-Smith (1985), but which seemed to us to be closely related to several of the taxa which he does consider to occur in North America. These included *Euphorbia cinerea* W.V. Fitzg., *Euphorbia condylocarpa* Bieb., *Euphorbia deflexa* Sibth. & Sm., *Euphorbia lingulata* Heuff., *Euphorbia platyphyllos* L., *Euphorbia purpurata* Thuill., *Euphorbia stricta* L., *Euphorbia taurinensis* All., and *Euphorbia variabilis* Cesati. A smaller, more homogeneous group of 30 OTUs representing 11 taxa was used to evaluate the methodology. In the smaller sample, one of the taxa were considered to be of hybrid origin and all the specimens were of European provenance. Table 2 lists the coding for the various OTUs, the scientific names of the taxa studied, and the individual sample sizes.

Table 1. Characters examined and method of assessing character states

Stem
- 1. Leaf scar size (mm)
- 2. Number of lateral branches

Leaves
- 3. Leaf base: cordate 5 4 3 2 1 acute
- 4. Leaf length (mm)
- 5-8. Leaf width at 1/4, 1/2, 3/4, 4/4 distance from base, respectively (mm)
- 9. Leaf apex: obtuse 1 2 3 4 5 acute
- 10. Length of longest vein (mm)

Inflorescence

A. Subtending bracts
- 11. Subtending bracts: cordate 1 2 3 4 5 acute
- 12-14. Bract width at 1/3, 2/3, 3/3 distance from base, respectively (mm)
- 15. Bract number
- 16. Longest bract in whorl (mm)
- 17. Shortest bract in whorl (mm)

B. Inflorescence bracts
- 18. Inflorescence bracts: cordate 1 2 3 4 5 acute
- 19-21. Bract width at 1/3, 2/3, 3/3 distance from base, respectively (mm)

C. Rays and flowers (cyathia)
- 22. Number of rays in main umbel
- 23. Average length of rays in main umbel (mm)
- 24. Number of flowers per umbel

D. Glands
- 25. Average number of glands per five cyathia
- 26. Degree of gland curvature: straight 1 2 3 4 5 curved

To assess phenetic relationships, a total of 26 characters often used in descriptions and keys were scored (Table 1)[2]. Dissimilarities (distances) were based on Gower's (1971) similarity coefficient for mixed data (Sneath and Sokal 1973). OTU by OTU similarities were converted to distance by setting $d = (1-s^2)^{1/2}$ (cf. Gower 1966*a*). Sorting algorithms included single linkage (nearest neighbour), unweighted centroid, weighted centroid (median), unweighted pair group using arithmetic averages (average linkage, UPGMA), complete linkage (furthest neighbour), weighted pair groups using arithmetic average, WPGMA), incremental sum of squares (Burr 1970), and flexible sort with $\alpha = 0.625$ (Lance and Williams 1967). These methods are discussed in full by Jardine and

Table 2. Index to OTU coding and sample size.

OTUs	Taxon	No. of samples
AG, AG1, etc.	*Euphorbia agraria* M. Bieb.	5
AL	*E. altaica* C.A.Meyer	1
AN, AN1	*E. androsaemifolia* Willd.	2
BES, BES1, etc.	*E. boissieriana* × *E. esula*	3
BO, BO1, etc.	*E. boissieriana* (Woron.) Prokh.	5
CI	*E. cinerea* W.V.Fitzg.	1
CO	*E. condylocarpa* Bieb.	1
CY1, etc.	*E. cyparissias* L.	16
DE, DE1	*E. deflexa* Sibth. & Sm.	2
ES, ES1, etc.	*E. esula* L.	53
GA, GA1, etc.	*E.* × *gayeri* Boros et Soo	4
GL	*E. glomerulans* Prokh.	1
IB	*E. iberica* Boiss.	1
LI	*E. lingulata* Heuff.	1
LU, LU1, etc.	*E. lucida* Waldst. & Kit.	9
MI	*E. microcarpa* Prokh.	1
NV, NV1	*E. nevadensis* Boiss. & Reut.	2
PA	*E.* × *paradoxa* (Schur) Podp.	1
PE, PE1, etc.	*E.* × *pseudoesula* Schur	14
PH	*E. platyphyllos* L.	1
PL, PL1	*E.* × *pseudolucida* Schur	2
PU	*E. purpurata* Thuill.	1
PV, PV1, etc.	*E.* × *pseudovirgata* (Schur) Soo	73
SA, SA1, etc.	*E. salicifolia* Host	6
ST	*E. stricta* L.	1
TA	*E. taurinensis* All.	1
TM	*E. tommasiniana* Bertol.	1
TS	*E. tschuiensis* (Prokh.)Serg.	1
UR	*E. uralensis* Fisch. ex Link	1
VA, VA1	*E. variabilis* Cesati	2
VI, VI1, etc.	*E. virgata* Waldst. & Kit.	16
WA	*E.* × *wagneri Soo*	1

[2] The data matrix for numerical taxonomic analysis may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

Sibson (1971*a*, 1971*b*), Williams *et al*. (1971), Sneath and Sokal (1973), and Clifford and Stephenson (1975). Principal coordinate analysis was used to ordinate the species using the Gower (1966*b*) method. Computations were carried out using programs supplied by the Engineering and Statistical Research Centre on the Digital VAX mainframe computer, Data Processing Division, Finance and Administration Branch, Agriculture Canada.

Results

Our results are presented in two parts. The first part consists of a detailed examination of the actual data set (Appendix) character by character. Table 3 summarizes the means and standard deviations of 14 characters which our analysis indicated varied significantly in the eight taxa for which we had five or more replicates. *Euphorbia boisseriana* was omitted because of its very consistent values. In a second part, the numerical analyses are summarized. Figures 1 and 3 illustrate the plots of OTUs on the first and second axes of the principal coordination, and Figs. 2 and 4 are the computer generated dendrograms of OTUs based on the incremental sum of squares method for the two sets of taxa treated.

Character variation

As shown in Table 3[3], some of the characters studied have relatively limited variability, while others do not. However, characters that have small standard deviations in an individual taxon may have identical means in species which are supposedly quite distinct. To illustrate this, we have organized the data into the following four categories: stem, leaf, inflorescence, and gland characters.

Stem characters

Leaf scar size (character 1) clearly segregates *E. cyparissias* and *E. lucida* from all the other taxa (Table 3). Other taxa purportedly closely allied to *E. esula* s.str. have overlapping values. Number of lateral branches (character 2) has been used by Moore (1958) to distinguish the hybrid *E.* × *pseudoesula* (many) from its *E. esula* parent (few or none). We found that this was a reliable character if one excludes PE3 and PE11 which had no lateral branches. We feel that these specimens were not correctly assigned by Radcliffe-Smith, and these are merely small-statured *E. esula*, which is supported by pollen stainability (96 and 87%, respectively). For the group as a whole, the number of lateral branches varied from 0 (in some OTUs codes AG, AL, DE, ES, GL, LU, MI, NV, PA, PE, PU, PV, SA, ST, TA, TS, VA, VI,) to 16 (ES24, PV55, PV65).

[3] Refer to footnote on previous page.

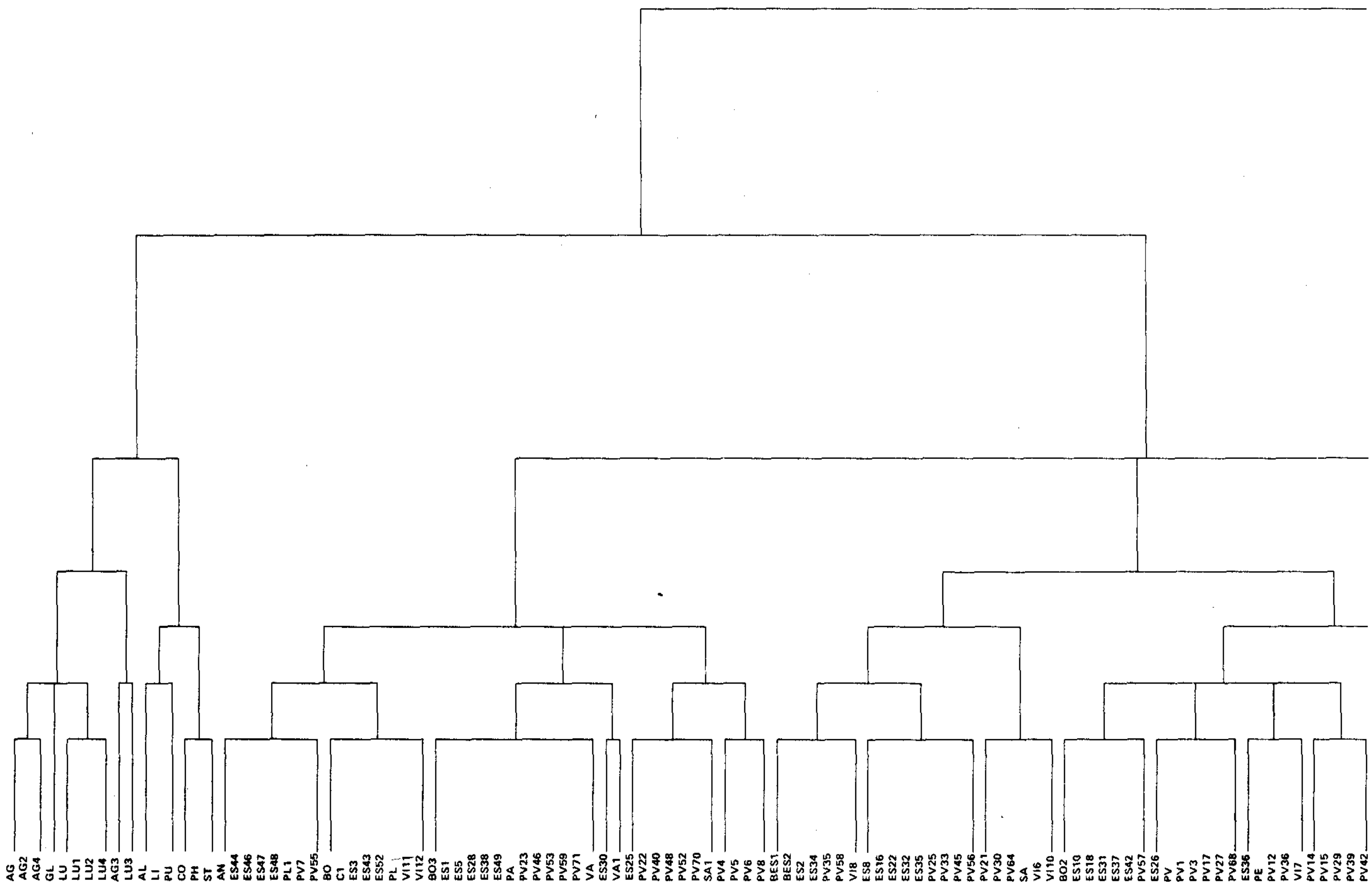

Fig. 1. Dendrogram showing computer-generated (incremental sums of square) tree of 200 OTUs of *Euphorbia esula* and 27 allied taxa.

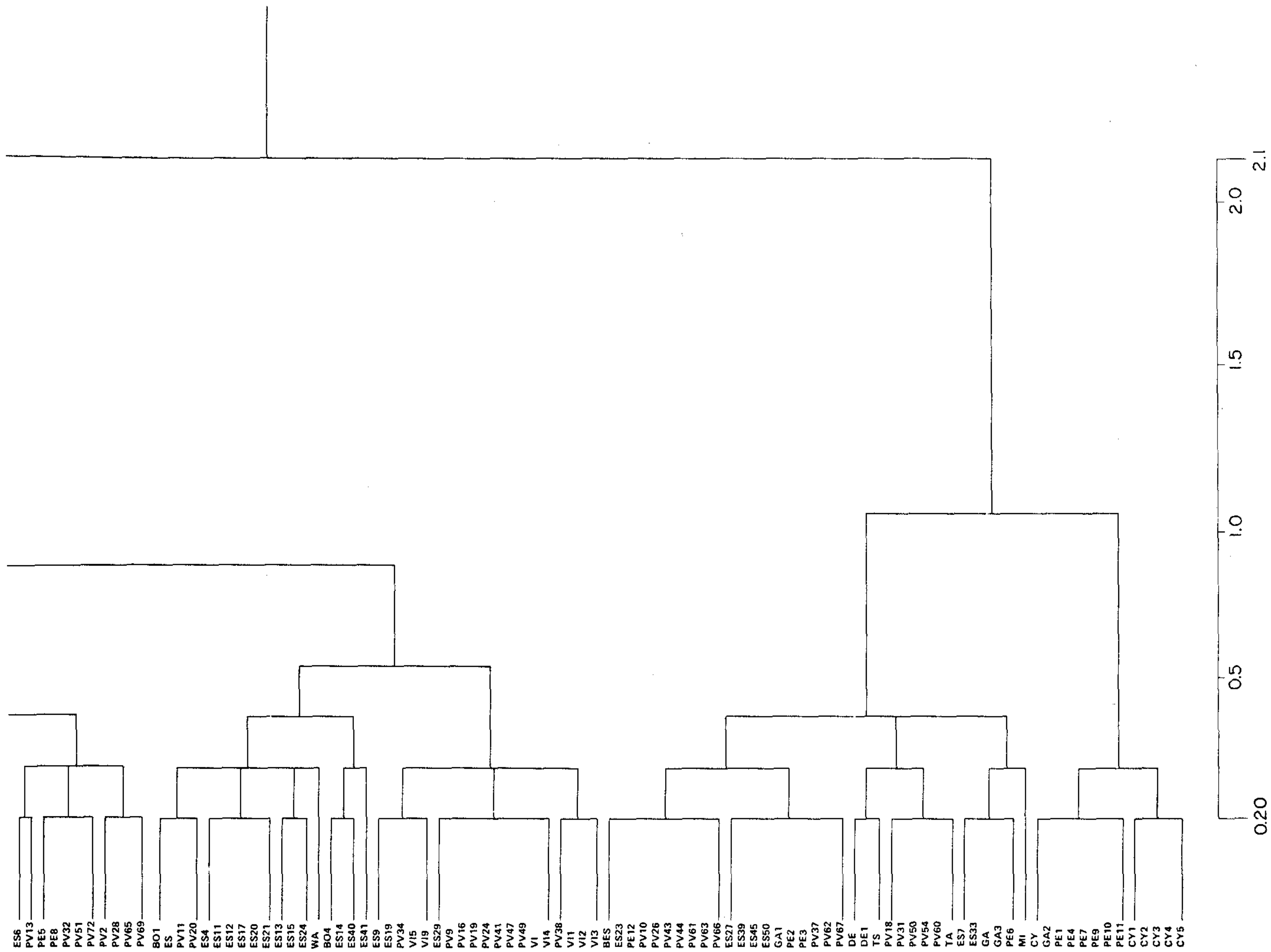

Fig. 1 (concluded)

Leaf characters

Leaf base shape (character 3) varied from cordate to acute (Table 3). *Euphorbia cyparissias, E. esula, E. × pseudoesula,* and *E. × pseudovirgata* had the most acute bases; *E. lucida, Euphorbia salicifolia* Host, and *E. virgata* had intermediate ones; *E. agraria* was the only taxon with a cordate base, a character which clearly separated it from all the other taxa. Leaf length (character 4) varied considerably: small-leaved OTUs included the DEs and CYs; large-leaved OTUs included VI12 and the LUs. Leaf length was not included in Table 3 because the leaf width character already indicated their relative shape. Leaf width was measured at quarterly intervals along the midrib (characters 5-8). The point of maximum width was reported to be an important diagnostic character for distinguishing the various leafy spurge taxa. None of the OTUs were widest at either the apex (character B) or the 1/4 point (character 5). Some, like AG, AG1, AG3, AG4, AL, BES-BES4, and LU-LUB, were widest at the midpoint (character 6). Although the occasional *E. esula* (e.g., ES5, ES6, and ES10) is widest at the 3/4 point (character 7), this is by no means characteristic of this taxon as is widely claimed (e.g., Radcliffe-Smith 1985). The values of the four width measurements considered together are indicative of leaf shape. *Euphorbia cyparissias* had the most linear leaves; *E. agraria* and *E. salicifolia* the least. Character 9 (leaf apex) exhibited the full range of character states from acute to obtuse. As a general rule, OTUs having small leaves tended to have acute apices (e.g., CY, PE, PV, and VI). Character 10 (length of longest lateral vein) was extremely variable. Not surprisingly, *E. cyparissias* had the shortest vein; *E. agraria* and *Euphorbia glomerulens* Prokh. had the longest veins; *E. esula, E. × pseudovirgata*, and *E. virgata* had intermediate values; and *E. × pseudoesula* had a value between that of its two parents. The extremely large standard deviation (SD = 5.25 mm) in *E. agraria* will be discussed in a later section.

Inflorescence characters

Bract shape (character 11) varied considerably; cordate subtending bracts occurred in GA, PE, and PV, TS, and VI samples, but the character itself was not consistent within a taxon. The largest value for mean number of bracts (character 15) was 18 in CY7 and CY16, 17 in CY6 and SA4, 16 in CY8, 15 in CY9, PV21, and SA5, and 14 in CY10, PE1, PE4, PE10, and SA. The lowest values were in DE, DE1, PV54, and VI15, each with 3, followed by AN1, BO, ES19, PH, PV18, ST, and TA with 4. *Euphorbia esula*, *E. × pseudoesula*, *E. × pseudovirgata*, and *E. lucida* all had overlapping values (Table 3). It is evident that this character can be quite inconsistent between plants of a single taxon; for example, individual plants of *E. agraria* had between 5 and 12 bracts. Length of longest bract (character 16) was highest in LI and ES14, and the smallest bracts were recorded for CY2, CY5, CY7, CY8, CY11, CY16, ES45, PV10, MI, TS, and UR. Characters 12-14 and 17-21 are omitted from Table 3 and the discussion because their deviation was quite constant. The number of umbel rays (character 22) was highest in CY16 with 20, CY6 and CY7 with 18, CY8 and SA4 with 17, SA with 16, and CY9, PV21, PV30, and SA5 each had 15; CY1, CY2, CY10, PE1, PE4, PE10, PE13, PV64, and VI6 all had 14 each. In contrast, DE1 and VI15 (3 each) and AN1, PH, PV18, and ST (4 each) had very

Table 3. Mean ± standard deviation of 13 characters and eight major OTUs.

Character No.	AG (*n* = 5)	CY (n = 16)	ES (*n* = 53)	LU (*n* = 9)	PE (*n = 14)*	PV (*n = 73)*	SA (*n* = 6)	VI (n = 16)
1	2.80±0.76	1.21±0.18	1.95±0.41	3.82±0.55	1.49±0.27	2.14±0.42	2.52±0.12	2.33±0.46
2	3.00±0.60	6.44±3.41	5.69±3.28	5.17±2.14	6.92±2.47	5.84±3.14	2.00±1.22	3.39±1.75
3	5.00±0.00	1.69±0.48	1.85±0.63	3.22±0.44	1.50±0.52	1.95±0.52	2.67±0.52	2.19±0.54
5	13.08±2.36	1.23±0.35	2.38±0.65	6.47±2.21	1.49±0.44	2.46±0.62	4.43±1.80	2.82±0.74
6	23.64±11.55	1.82±0.49	6.77±2.74	18.06±5.43	3.05±0.95	5.35±1.24	17.22±6.77	5.90±1.72
7	18.12±10.95	1.64±0.38	6.00±2.40	13.47±4.16	2.91±0.69	4.78±1.09	13.95±5.93	4.98±1.42
8	4.22±1.61	0.88±0.27	2.04±0.83	3.52±1.57	1.22±0.37	2.03±0.56	3.38±2.05	1.85±0.53
9	2.40±1.34	3.88±0.81	3.19±1.30	3.00±0.87	4.14±0.77	4.19±0.71	3.00±0.63	4.75±0.45
10	13.30±5.25	1.71±0.42	6.76±2.01	11.80±3.30	3.51±0. 99	6.52±1.69	9.87±3.50	6.85±3.30
15	8.40±2.88	13.06±2.86	7.24±1.45	8.00±1.32	10.92±2.37	8.00±1.89	13.17±2.64	7.94±2.21
22	8.40±2.61	13.88±3.01	7.45±1.42	7.78±1.48	11.43±2.44	8.10±2.06	13.67±2.81	8.44± 2.85
23	36.80±4.46	24.54±13.32	55.37±32.46	39.29±22.43	37.54±14.62	40.49±19.47	45.52±24.66	52.81±29.00
24	32.00±10.00	44.19±11.55	27.47±7.98	31.33±9.49	37.50±12.48	27.48±9.30	50.17±13.78	31.13±12.55

NOTE: Characters corresponding to numbers are described in Table 1.

low values. The largest value of average length of rays in the main umbel (character 23) was found in ES8, and the smallest in CI, CY5, CY15, CI, NV1, and PV60. This character varied greatly within a single taxon and the standard deviations were quite large (Table 3). The mean number of flowers per umbel (character 24) was highest in SA4 (70), PE13 (65), CY13 and CY16 (60), CY6 (58), VI1, VI2, IB, and SA2 (56), BY8 and PV21 (55), CY7 (53), and PE9 and SA5 (52). Small values occurred in BO (5), AL (7), and GA, PV60, VA, and VA1 (8 each). Note that the values varied widely within a given taxon (e.g., GA had 8-35 flowers per umbel). The average in *E.* × *pseudoesula* was between that of the two parents (Table 3).

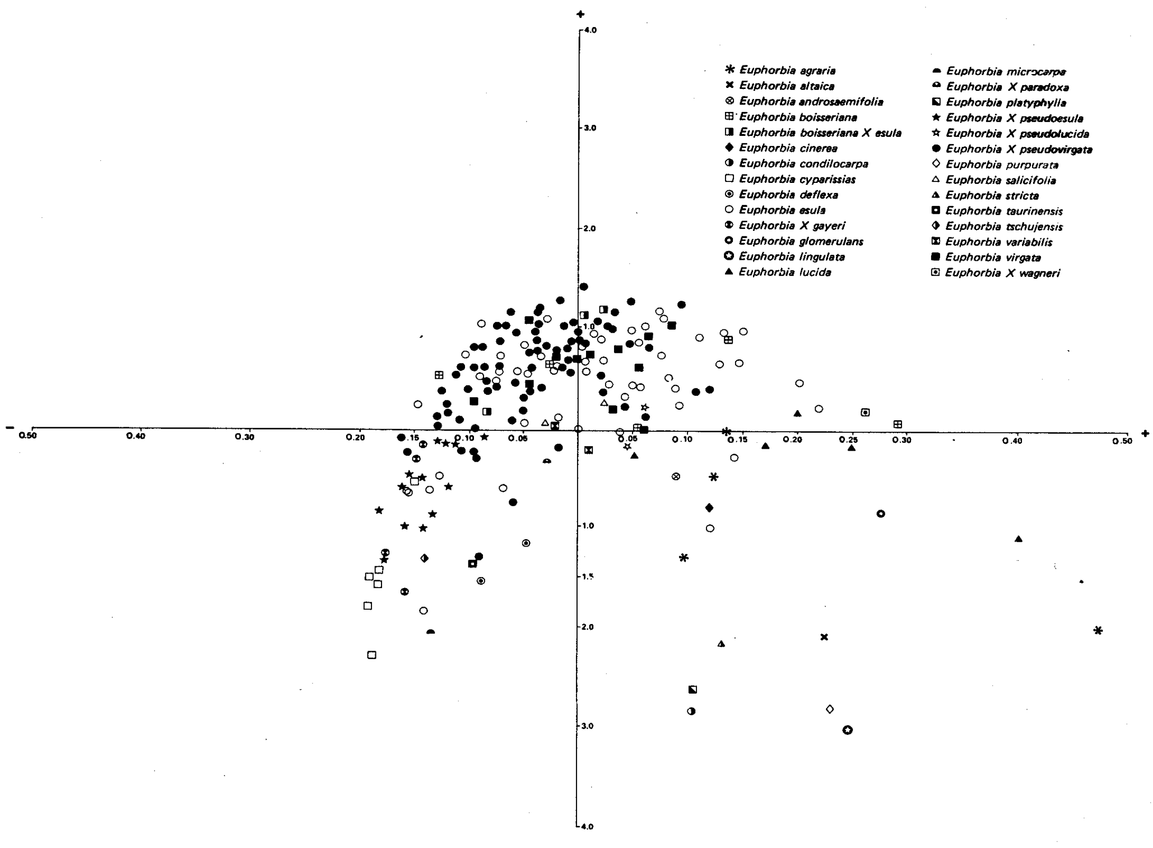

Fig. 2. Principal coordinate analysis graph on the first two axes of 200 OTUs of *Euphorbia esula* and 27 allied taxa.

Gland characters

Gland number per five cyathia were scored; the average number was 19.84 glands. Most OTUs had four glands per cyathium. However, VI2 had one cyathia with five glands, VI8 had three cyathia with five glands, and PE1 had one with three glands. Gland number (character 25) was fairly constant and curvature of glands (character 26), a supposed important character, when scored showed absolutely no variation and therefore was not included in the final analysis.

Numerical taxonomic analysis

Owing to the large overlap in the values scored[4], the dendrograms based on most of the sorting algorithms exhibited no structure. However, the incremental sums of squares dendrograms (Figs. 1, 3) did and gave results very similar to those obtained in the principal coordinate analysis (Figs. 2, 4). Several groups could be detected. *Euphorbia cyparissias*, *E. agraria, E. lucida*, and *E. salicifolia* were separated by the ordination analysis, and on the first two axes in the principal coordinate analysis. In contrast, no distinct clusters were evident in the OTUs representing the taxa belonging to *E. esula* s.l. (*E. esula* s.str., *E. virgata*, *E.* × *pseudovirgata*, *E. boissieriana*, etc.), and their indices of dissimilarity (BES, ES, PV, VI, etc.) were very close. OTUs representing E. × *pseudoesula* (PE), the putative hybrid between *E. esula* and *E. cyparissias*, formed a cluster between the two supposed parents. On the other hand, OTUs representing other purported hybrid taxa (e.g., *E.* × *pseudovirgata* = *E. esula* × *E. virgata*; *E.* × *wagneri* = *E. esula* × *E. lucida*) did not lie between the putative parents.

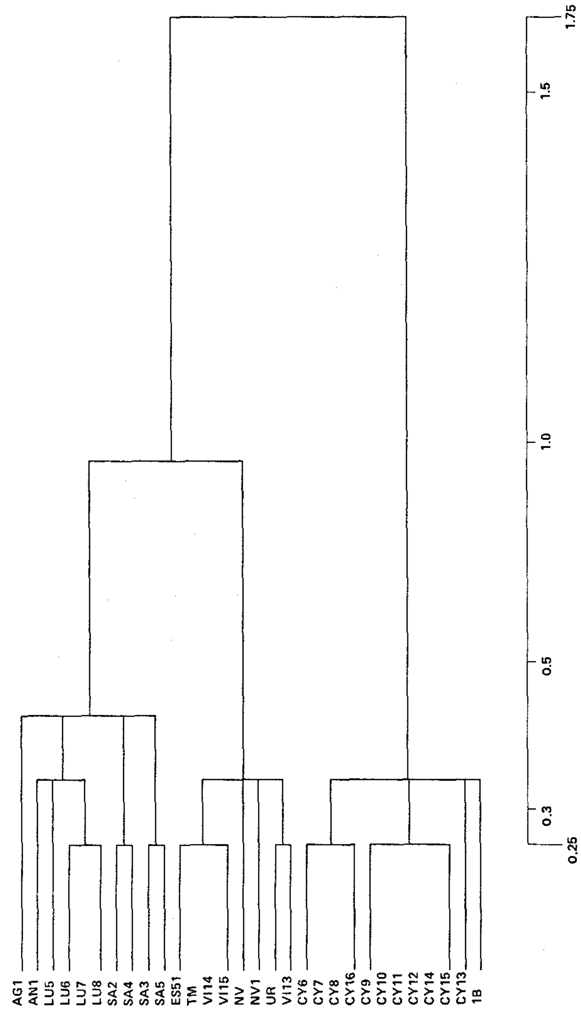

Fig. 3. Dendrogram showing computer-generated tree (incremental sums of square) of 30 OTUs of *Euphorbia esula* and 11 allied taxa which can readily be identified using keys to European material.

Discussion

Variation in leafy spurge and its allies

Taxonomists differ as to the number of species they recognize in section *Esula* of subgenus *Esula*. Estimates range from a few (e.g., Webster 1967) to a maximum of 79

[4] Refer to footnote on p. 6.

species and hybrids (Radcliffe-Smith 1985). Principal coordinate analysis and incremental sum of squares clustering were used to evaluate these divergent points of view by determining the number of distinct clusters which could be detected. The test sample of 200 OTUs encompassed a wide range of North American and European material, and included a number of specimens annotated by various authors of well-known treatments of the group. *Euphorbia agraria, E. cyparissias, E. lucida*, *and E. salicifolia* were separated by our techniques. A number of these taxa possess at least one distinct character. *Euphorbia agraria* is the only species which has cordate leaf bases*, E. salicifolia* is the only species which has cordate leaf bases, *E. salicifolia* is the only species with pubescent leaves, and *E. lucida* is the only one with shiny laminae. In contrast, the taxa (e.g., *E. esula s.str., E. boissieriana, E. virgata*) into which Radcliffe-Smith (1985) subdivided *E. esula* had indices of dissimilarity so close that our analyses were unable to separate them into groups. With respect to the techniques used, it should be pointed out that cluster analysis is the numerical taxonomic technique most widely used for obtaining groupings. The incremental sums of squares method will normally separate variation of its midpoint and when OTUs are scattered, the method will cluster groups (Duncan and Baum 1981). The Lefkovitch (1976) method used in this study consolidates OTUs into clusters (Duncan and Baum 1981). Therefore, the computer generated dendograms (Figs. 2, 4) are indicative of the actual groups present in the leafy spurge aggregate.

The NT results are supported by our cytogenetic studies (Stahevitch *et al*. 1988*b*). Most leafy spurge populations we examined were hexaploid with n = 30, which agreed with earlier studies (Moore 1958; Pritchard 1958). Meiosis was regular with 30 bivalents at metaphase I. Occasionally, anomalous numbers have been reported in the literature. Loon and De Jong (1978) found 2*n* = 16 in material collected in France, but their voucher (Loon 10675, U!) proved to be *Euphorbia segetalis* L. for which this chromosome number has been reported frequently. Other chromosome numbers include 2*n* = 20, 56, and 64 (Baksay 1958; Hurusawa and Shimoyama 1976), but no vouchers are available for assessment. In contrast, cypress spurge (*E. cyparissias*) is diploid and tetraploid (2*n* = 20, 40) and *E. agraria* is tetraploid with 2*n* = 40 (Stahevitch *et al*. 1988a*). Euphorbia lucida* and *E. salicifolia* are reported to have a sporophytic chromosome number of 2*n* = 18 (Polya 1950). Thus, chromosome numbers per se act as a barrier between some species, but do not provide a barrier to gene exchange within *E. esula* s.l. Furthermore, all our crossing experiments between samples of *E. esula* s.l. were successful, and meiosis in the F_1 progeny was normal, lending further evidence that these represent a single interbreeding population.

The NT analyses also did not indicate widespread hybridization. *The E.* × *pseudoesula* cluster does lie midway between the two parental groups, *E. cyparissias* and *E. esula*. The hybrid origin of this variant is supported by cytological evidence (Moore 1958). Other putative hybrids do not exhibit a similar pattern. For example, OTUs representing *E.* × *pseudovirgata* and its purported parents, *E. esula* and *E. virgata*, more or less overlap. The OTUs representing *E.* × *gayeri* are intermediate between *E. cyparissias* and *E.* × *pseudovirgata* rather than between the former and *E. virgata*, as Radcliffe-Smith's treatment demands. Pollen stainability approached 100% in most of the specimens purportedly of hybrid origin, with the exception of those of *E.* × *pseudoesula* (Stahevitch *et al*. 1988*b*). All these results support a conservative treatment of the group.

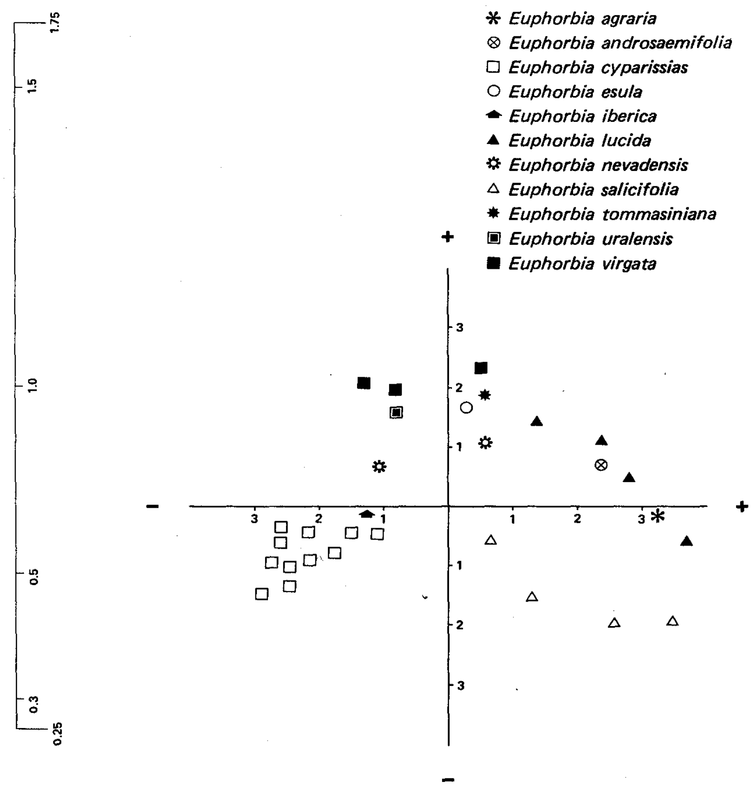

Fig. 4. Principal coordinate graph of 30 OTUs of *Euphorbia esula* and 11 allied taxa in Europe.

The criteria used to ascribe hybrid origin are unclear to us. A number of specimens collected in the Hawkesbury-L'Orignal area of eastern Ontario were assigned by Radcliffe-Smith to several taxa, namely *E. esula* s. str., *E.* × *gayeri*, *E.* × *pseudoesula*, *E.* × *pseudovirgata*, and *E. virgata* s.str. Consultation with the collectors indicated that these were gathered at a single locality (the Cass Farm). Returning to the site, we found that different shoots of the same plant were identical to purportedly different taxa. Perhaps even more disturbing was material (DAO 38176 and DAO 38174) from this site originally identified by Moore as "*E. esula*" which had been annotated "*E.* × *pseudoesula,*" but which had a chromosome number of $2n = 60$ (*E. esula*), and not $2n = 50$ (*E.* × *pseudoesula).*

There is no doubt that leafy spurge is morphologically quite variable. Croizat (1945) conjectured that much of this variation has a phenological or environmental rather than genetic basis. Raju (1985) undertook an extensive study of leafy spurge anatomy. He demonstrated experimentally that variants in leafy spurge morphology represented different developmental phases in the compound dichaseum. Shoots having different inflorescence types and leaf shapes appeared on the same plants at different stages of development. Plants subjected to several fertilizer treatments produced more robust growth forms.

Nomenclature and leafy spurge

In the course of the present study, we had the opportunity to examine photographs of a number of nomenclatural type collections. The following observations may be of interest.

Euphorbia esula* and *E. virgata

There is a widespread misapprehension that Linnaean collections of *E. esula* consist entirely of plants with leaves broader above the middle and that F.A. von Kitaibel's collections of *E. virgata* are all narrow-leaved plants. Photographs of three Linnaean specimens of *E. esula* (Savage catalogue Nos. 630.62-630.64) were examined. Radcliffe-Smith had designated the first, a broad-leaved plant, as the nomenclatural type. On the other hand, the Savage catalogue Nos. 630.63 and 630.64 sheets contain a mixture of branches with broad-spatulate, linear, and linear-lanceolate leaves. We also found similar variation in the eight Kitaibel specimens from BP. Thus, contrary to the impression left by much of the literature, neither Linnaeus (1753) nor Waldstein and Kitaibel (1804) seem to have based their con concepts of *E. esula* and *E. virgata* on leaf width or leaf shape, We suspect that Waldstein and Kitaibel really intended to contrast dull green ("*virgata*") with gray shiny ("*lucida*") leaves. The recognition of broad-leaved and narrow-leaved plants as distinct species (*E. esula* and *E. virgata*) appears to have erroneously been attributed to Waldstein and Kitaibel by later taxonomists (beginning with Sprengel 1825).

Euphorbia agraria, E. lucida,* and *E. pseudoagraria

There has been some confusion in the North American literature concerning the first two species. Croizat (1945) stated that both were present in North America, particularly that *E. agraria* was found in New York and *E. lucida* at Edgerton, Alberta. We found that the latter actually are misidentified plants of *E. agraria* (e.g., AG3). Since Croizat was acquainted with both species, we surmise that he never actually examined collections from Edgerton, This population is now extinct, but we did find another *E. agraria* population at Lonely Lake on the Bow River in Alberta. The only other Canadian specimen we have seen labelled "*E. lucida*" is a robust specimen of *E. esula* collected at Fort Saskatchewan, Alberta (ES in our analyses).

G. Wheeler called our attention to the very long leaves on the material collected at Lonely Lake compared with the Edgerton population and suggested that the name *E. pseudoagraria* rather than *E. agraria* might apply to this population. None of the five specimens of *E. pseudoagraria* we examined, including the type (Smirnov s.n. 15-5-38) and three topotypes (Smirnov s.n. 10-5-38, 11-5-38, 3-6-38), had leaves with even vaguely cordate bases. Furthermore, when grown under greenhouse conditions, the Lonely Lake plants eventually reverted to the short-leaved form typical of *E. agraria*. Leaves produced late in the growing season tended to be longer than early leaves. The leaf base, however is cordate regardless of the season.

Conclusion

The NT analyses we carried out in the present study indicates that the variation in leafy spurge is continuous. Our cytogenetic analysis (Stahevitch *et al*. 1988*b*) detected a similar pattern, since no breeding barriers were present between populations and the F_1 progeny exhibited normal meiosis. The biological data suggest that leafy spurge, although variable, is a single species which, according to the rules of nomenclature, should bear the name *E. esula*. The excessive splitting that has characterized most recent treatments of this group is perhaps best seen as part of a broader historical trend that has characterized European taxonomy recently (e.g., *Taraxacum*; Richards and Sell 1976). Similarly, the splitting on minutae, which characterized the treatment by Schur (1858, 1866), reflects an earlier such trend in Central European taxonomy during the middle of the last century (Mayr 1982).

Our NT analyses showed that in addition to leafy spurge, several other taxa are present. Leafy spurge and its allies can be identified as follows:

1. Leaf base cordate .... *E. agraria*
1. Leaf base not cordate 2

2. Plants puberulent .... *E. salicifolia*
2. Plants glabrous 3

3. Leaf blade shiny .... *E. lucida*
3. Leaf blade not shiny 4

4. Cauline leaves greater than 4 mm wide, lateral branches at most a few with scattered leaves .... *E. esula*
4. Cauline leaves less than 4 mm wide, lateral branches many with congested leaves 5

5. Cauline leaves not more than 2.6 mm wide; terminal pseudocymes in compact clusters, lateral branches absent or few .... *E. cyparissias*
5. Cauline leaves greater than 2.6 mm wide; terminal pseudocymes in open clusters, lateral branches numerous .... *E. ×pseudoesula*

Four of these taxa occur in Canada, namely *E. esula*, *E.* × *pseudoesula* (the hybrid between *E. esula* and *E. cyparissias*), *E. agraria*, and *E. cyparissias*. As was discussed in the foregoing section, we have seen no authentic record of *E. lucida* in Canada. Likewise, we found no evidence in the field or herbarium *of E. salicifolia* occurring here.

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References

Bakke, A. L. 1936. Leafy spurge, *Euphorbia esula* L. Iowa State Coll. Agric. Exp. Stn, Res. Bull. No. 198. pp. 209-246.

Baksay, L. 1958. The chromosome numbers of Ponto-Mediterranean plant species, Ann. Hist. Nat. Mus. Natl. Hung. (Ser.Nov. 9), 50:121-125.

Best, K. F., Bowes, G. G., Thomas, A. G., and Maw, M. G. 1980. The biology of Canadian weeds. 39. *Euphorbia esula* L. Can. J. Plant Sci. 60:651-663.

Boissier, E. 1862. Euphorbieae. *In* Prodromus systematis naturalis regni vegetabilis. Vol. 15(2). (Facsimile edition, 1966.) *Edited by* A. P. De Candolle. Crammer, Lehre. pp. 3-188.

Boivin, B. 1967. *Euphorbia* L. In Flora of the prairie provinces. Phytologia, 15:444-446.

Britton, N. L. 1921. The leafy spurge becoming a pest. J. N.Y. Bot. Gard, 22:73-75.

Burr, E. H. 1970. Cluster sorting with mixed character types. Aust. Comput. J. 2:98-103.

Clifford, H. T., and Stephenson, W. 1975. An introduction to numerical classification. Academic Press, New York.

Croizat, L. 1945. "*Euphorbia esula*" in North America. Am. Midl. Nat. 33:231-243.

Duncan, T., and Baum, B. R. 1981. Numerical phenetics: its uses in botanical systematics. Annu. Rev. Ecol. Syst. 12:387-404.

Dunn, P. H. 1979. The distribution of leafy spurge (*Euphorbia esula*) and other weedy *Euphorbia* spp. in the United States. Weed Sci. 27:509-516.

Dunn, P. H. 1985. Origins of leafy spurge in North America. *In* Leafy spurge. *Edited by* A. K. Watson. Monogr. Ser. No. 3, Weed Science Society of America, Champaign, IL. pp. 1-13.

Dunn, P. H., and Radcliffe-Smith, A. 1982. The variability of leafy spurge (*Euphorbia* spp.) in the United States. *In* North Central Weed Control Conference Proceedings Vol. 37. pp. 48-53.

Ebke, D. H., and McCarty, M. K. 1983. A nursery study of leafy spurge (*Euphorbia* spp.) complex from North America. Weed Sci. 31:866-873.

Fernald, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., New York.

Fischer, F. E. 1822. "*Euphorbia uralensis*". *In* Enumeratio plantarum horti regii botanici berolinensis altera. Vol. 2. *Edited by* J. H. Link. Berlin. p. 14.

Frankton, C., and Mulligan, G. A. 1987. Weeds of Canada. NC Press, Toronto.

Gower, J. C. 1966*a*. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika, 53:325-388.

Gower, J. C. 1966*b*. A Q-techniqué for the calculation of canonical variates. Biometrika, 53:588-590.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics, 27:857-874.

Groh, H. 1935. Leafy spurge-*Euphorbia esula* or *virgata*? Sci. Agric. 15:701-703.

Harris, P. 1984. *Euphorbia esula-virgata* complex, leafy spurge and *E, cyparissias* L., cypress spurge (Euphorbiaceae). *In* Biological control programmes against insects and weeds in Canada (1969-1980). *Edited by* J. S. Kelleher and M. A. Hulme. Commonwealth Agricultural Bureau, Slough. pp, 159-169.

Hitchcock, C. L., Cronquist, A., Owenby, M., and Thompson, J. W. 1961. *Euphorbia* L. *In* Vascular plants of the Pacific Northwest. Part 3. University of Washington Press, Seattle. pp. 395-401.

Holmgren, P. K., Keuken, W., and Schofield, E. K. 1981. Index herbariorum. Dr. W. Junk B.V., The Hague.

Hurusawa, I., and Shimoyama, S. 1976. Die Mannigfaltigkeit der Chromosomenzahl bei der Gattung *Euphorbia*. Beitr. Biol. Pflanz. 52:255-266.

Jardine, N., and Sibson, R. 1971*a*. Mathematical taxonomy. J. Wiley & Sons, London.

Jardine, N., and Sibson, R. 1971*b*. Choice of methods for automatic classification. Comput. J. 14:404-406.

Klokov, M. V. 1955. *Euphorbia* L. *In* Flora U.R.S.R., vol. 7 (in Ukrainian). *Edited by* M. V. Klokov and O. D. Visulin. Akademia Nauk Ukrainskoi, Kiev. pp, 121-176.

Lance, G. N., and Williams, W. T. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. Comput. J. 9:373-380.

Lefkovitch, L. P. 1976. Hierarchical clustering from principle coordinates: an effective method for small to very large numbers of objects. Math. Biosci. 31:157-174.

Linnaeus, C. 1753. Species plantarum. (Facsimile edition, 1959). Vol. 2. Bartholomew Press, London.

Loon, J. C. Van, and De Jong, H. 1978. *In* IOPB chromosome number reports. LIX. Taxon, 27:53-61.

Lym, R. G., and Kirby, D. R. 1987. Cattle foraging behavior in leafy spurge *Euphorbia-esula* infested rangeland. Weed Technol. 1(4):314-318.

Mayr, E. 1982. The growth of biological thought. Harvard University Press, Cambridge, MA.

Moore, R. J. 1958. Cytotaxonomy of *Euphorbia esula* in Canada and its hybrid with *Euphorbia cyparissias*. Can. J. Bot. 36:547559.

Morton, C. V. 1937. The correct name of leafy spurge. Rhodora, 39:49-50.

Ostenteld, A. 1903. *Euphorbia esula* L. Ogdens Slaegtninge. Bot. Not. 1903:125-127.

Packer, J. G. 1983. *Euphorbia* L. *In* Flora of Alberta. 2nd rev. ed. University of Toronto Press, Toronto. pp. 395-396.

Polya, L. 1950. Chromosome numbers of some Hungarian plants. II. (In Hungarian.) Ann. Biol. Univ. Debreceniens. 1: 46-56.

Pritchard, T. 1958. The genecology of weed species. Studies on *Euphorbia cyparissias* L. and *Hypericum perforatum* L. Ph.D. thesis, University of Leeds, Leeds.

Pritchard, T. 1960. Race formation in weedy species with especial reference to *Euphorbia cyparissias* L. and *Hypericum perforation* L. *In* Biology of weeds. *Edited by* J. L. Harper. Blackwell Scientific Publications, Oxford. pp. 61-68.

Pritchard, T. 1961. The cytotaxonomy of the weedy species *Euphorbia cyparissias* L. and *Euphorbia esula* L. Recent Adv. Bot. (9th Int. Bot. Congr.) 1:866-870.

PRODAN, I. 1953. *Euphorbia* L. *lit* Flora repulicii popullare Romane. Vol. 2. (in Romanian.) *Edited by* N. T. Savulescu. Editura Academici Republicii Populate Romani, Bucaresti. pp. 296-367.

Prokhanov, Y, 1. 1949. Genus 856. *Euphorbia L*. *In* Flora of the USSR. Vol, 14. *Edited by* B. K. Shishkin. English translation, 1974, Israel Programme or Scientific Translations, Jerusalem. pp. 233-378.

Radcliffe-Smith, A. 1985. Taxonomy of North American leafy spurge. *In* Leafy spurge. *Edited by* A. K. Watson. Monogr. Ser. No. 3, Weed Science Society of America, Champaign, IL. pp. 14-25.

Raju, M. V. S. 1985. Morphology and anatomy of leafy spurge. *In* Leafy spurge. *Edited by* A. K. Watson. Monogr. Ser. No. E. Weed Science Society of America, Champaign, IL. pp. 26-41.

Richards, A. J., and Sell, P. D. 1976. *Taraxacum Weber*, *In* Flora Europaea. Vol. 4. *Edited by* T. G. Tutin *et al*. Cambridge University Press, Cambridge. pp. 332-343.

Rousseau, C. 1968. Histoire, habitat et distribution de 220 plantes introduites au Quebec. Nat. Can. (Que.), 95: 49-169.

Schur, J. F. 1858. Sertum florae Transsilvaniae. Verb. Miltheil. Siebenb. Ver. Naturwiss. Hermannstadt, 4: 66.

Schur, J. F. 1866. Enumeratio plantarium Transsilvaniae. Vienna. pp. 591-600.

Smith, A. R., and Tutin, T. G. 1968. *Euphorbia* L. *In* Flora Europaea. Vol. 2. *Edited by* T. G. Tutin *et al*. Cambridge University Press, Cambridge, pp. 213-226.

Sneath, P. H. A., and Sokal, R. R. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

Soo, R. Von. 1925. *Euphorbia*. Bot. KozI, 22:66-67.

Soo, R. Von. 1930. Vergleichende Vegetationstudien Zentralalpen-Karpathen Ungarn. Veroeff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Ruebel Zuer. 6:252.

Soo, R. Von. 1980. A magyar flora es vegetacio rendszerani-novenyfoldrajzi kezikonyve. Vol. 6. Akademiai Kiado, Budapest.

Sprengel, K. P. J. 1825. Linnaei Systema Vegetabilium. 6th ed. Vol. 3.

Stahevitch, A. E., Crompton, C. W., and Wojtas, W. A. 1988*a*. Biology of Canadian weeds. *Euphorbia cyparissias* L. Can. J. Plant Sci. 68:175-191.

Stahevitch, A. E., Crompton, C. W., and Wojtas, W. A. 1988*b*. Cytogenetic studies of leafy spurge, *Euphorbia esula*, and its allies (Euphorbiaceae). Can. J. Bot. 66:2247-2257.

Waldstein, F. A. Von, and Kitaibel, P. 1904. Descriptiones et icones Plantarum rariorum Hungariae. Vol. 2. p. 176.

Watson, A. K. 1985. Introduction-the leafy spurge problem. *In* Leafy spurge. *Edited by* A. K. Watson. Monogr. Ser. 3, Weed Science Society of America, Champaign, IL. pp. 1-6.

Webster, G. L. 1967. The genera of *Euphorbiaceae* in the Southwestern United States. J. Arnold Arbor. Harv. Univ. 48: 363-430.

Williams, W. F., Clifford, H. T., and Lance, G. N. 1971. Groupsize dependence: a rationale for choice between numerical classifications. Comput. J. 14:157-162.

Zimmermann, W. 1924. *Euphorbia* L. (=*Tithlymalus* Tourn.). Wolfsmilch. *In* Illustrierte Flora von Mitteleuropa. Vol. 5, Part 1. *Edited by* G. Hegi. J. F. Lehmanns Verlag, Munich. pp. 134-190.