

THE SYSTEMATICS OF
ROCKY MOUNTAIN MAPLE, *ACER GLABRUM* TORR.

by

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Abstract

The Systematics of Rocky Mountain Maple, *Acer glabrum* Torrey

by Douglas Edward Clive Justice

This study was undertaken to determine the most appropriate infraspecific taxonomy for *Acer glabrum*, as a review of the recent literature showed that the biological and taxonomic validity of the infraspecific taxa of *Acer glabrum* is not clear. This study involved field and herbarium studies, morphometric analysis, common garden transplant experiments and foliar flavonoid analysis.

Field and herbarium studies showed that subsp. *siskiyouense*, var. *greenii* and var. *tripartitum*, names common in the literature, do not represent valid taxa. Varieties *diffusum*, *douglasii*, *glabrum*, *neomexicanum*, and *torreyi* are recognized, and have distinguishing leaf morphological characters that are correlated with more or less discrete geographical ranges. Morphometric analysis showed that leaf morphology is geographically correlated, but some numerical methods are not able to discriminate all taxa. Transplant experiments suggest that the distinctive morphologies of the early leaves of individual taxa are genetically fixed, and that late leaves, subject to environmental constraints, all tend toward a single morphology. Flavonoid analysis showed that there is no variation within or among the infraspecific taxa. The presence of flavanones strengthens the presumed close relationships between sections *Glabra*, *Arguta*, *Cissifolia* and *Indivisa*.

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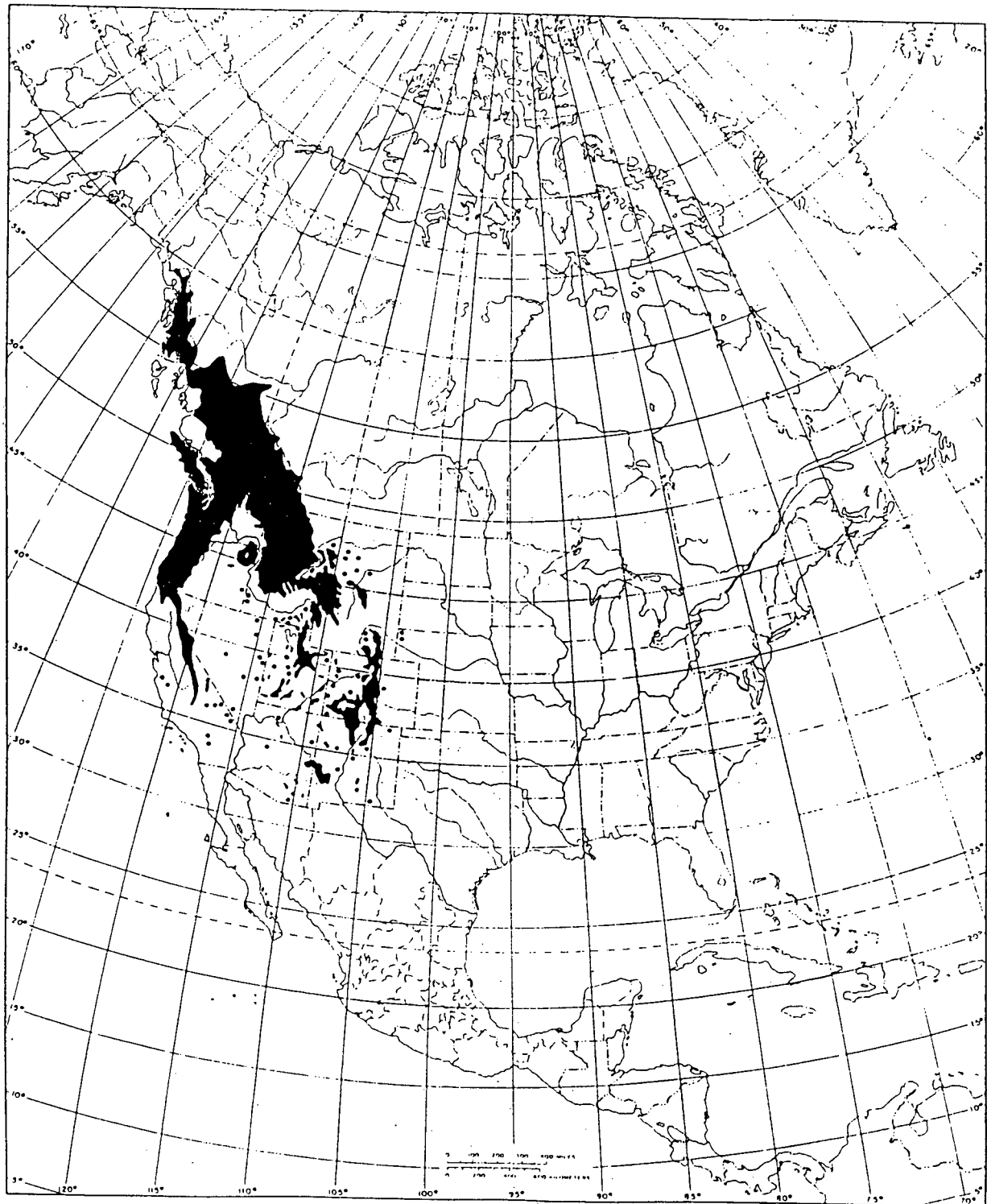
Rocky Mountain maple has the most northerly distribution of any North American maple (Little, 1985), and is the most widely distributed maple in western North America (Figure 1.1.). It occurs in Alaska, British Columbia, Alberta and every continental state of the United States from the Rocky Mountains to the Pacific Ocean.

Rocky Mountain maple, *Acer glabrum* Torrey, is the only species in *Acer* section *Glabra* Pax. Its specific status has not been questioned, nor have any of its extant taxa been recognized at the specific level since Greene (1902). A large number of subspecies or varieties have been described, however, and some of these have distinctive allopatric ranges. These infraspecific taxa are all characterized primarily by leaf morphology, except for var. *greenii*, which is based on a fruit character. As the biological and taxonomic validity of these infraspecific taxa is not clear, this study was undertaken to determine the most appropriate infraspecific taxonomy for the species. The study involved:

1. Field Studies
2. Herbarium Studies
3. Morphometric Analysis
4. Common Garden Transplant Experiments
5. Flavonoid Analysis

Currently recognized infraspecific taxa are distinguished on the basis of leaf morphology; therefore, leaf characters were emphasized in morphological and morphometric analyses. Because many of the alleged morphological differences could be caused by environmental factors — specifically water availability — phenotypic plasticity was investigated in common garden transplant experiments using seedlings and grafted scions.

Figure 1.1. Range of *Acer glabrum* Torrey (from Little, 1976)



Heterophylly was investigated in natural populations and in the plants cultivated in the transplant experiments. Foliar flavonoid analysis was undertaken to determine the extent of qualitative flavonoid variation among infraspecific taxa; findings of this analysis have been accepted for publication (Justice *et al*, 1995). Infraspecific taxa currently recognized, and their reported distinguishing features, are presented in Table 1.1.

Table 1.1. *Acer glabrum* Intraspecific Taxa (after Keller [1942] and Murray [1983])

taxon	morphology	distribution
<i>diffusum</i>	Leaves leathery, less than 3 cm wide, 3-5-lobed or 3-parted, with few blunt marginal teeth; shrubby, <4m; twigs whitish.	W. Utah to E. and S. California (W. Great Basin)
<i>douglasii</i>	Three-5-lobed leaves with thin, broad (up to 18 cm across) lamina and shallow, mostly obtuse lobes and sinuses; shrubby to tree-like, to 15m; twigs reddish or greyish.	S.E. Alaska to Wyoming and N. border of California (N.W. N. America)
<i>glabrum</i>	Leaves 4-6 cm across with prominent marginal teeth and acute lobes; shrubby to tree-like, 3-8m; twigs reddish or greyish.	mostly Wyoming and Colorado (cent. Rocky Mountains)
<i>greenii</i>	Leaves less than 5 cm across, 3-lobed to 3-parted; shrubby, <4m; twigs greyish; overlapping seed-wings.	Tulare County, California (S. Sierra Nevada)
<i>neomexicanum</i>	Leaves 5-10.5 cm across, mostly ternate, glaucous beneath; shrubby to tree-like, 3-8m; twigs reddish.	Colorado, New Mexico, S.E. Utah, S.E. Arizona (S. Rocky Mountains)
<i>siskiyouense</i>	Leaves with 3-5 rhombic lobes; intermediate between varieties <i>torreyi</i> and <i>douglasii</i>	N. California and S. Oregon (Siskiyou Mountains)
<i>torreyi</i>	Leaves with deeper, acute sinuses and lobes apically rounded in outline, parted often more than half their length; shrubby to tree-like, 3-8m; twigs reddish.	S. border Oregon to L. Tahoe and S. California (Sierra Nevada)
<i>tripartitum</i>	Leaves less than 4 cm across, 3-lobed with the lobes parted almost to the petiole; shrubby, <4m; twigs greyish.	W. Wyoming to N.E. Nevada and S. cent. Utah (E. Great Basin)

2.1. Field and Herbarium Studies

Collections

Samples of *A. glabrum* were collected from populations throughout western North America between September of 1993 and July 1994 (Table 2.1.1.). One to 4 populations from each of 7 infraspecific taxon localities were sampled (Figure 2.1.1.). Taxon localities are known habitats of infraspecific taxa according to Keller (1942) and Murray (1983). Populations are represented by collections of between 2 and 20 leaves per tree, from each of 8 to 10 trees per site visited. Leaves and branches were collected from randomly selected trees, characterized and pressed. All phases of leaves were collected where present. Available scions and fruit were also collected, and subsequently stored. Seed collected in New Mexico in 1992 by P. Kelaidis of the Denver Botanic Garden was also used in this study.

Infraspecific taxon localities not visited on collecting trips in this study are represented by herbarium specimens. Herbarium specimens used for morphometric analysis were selected on the basis of the greatest number of individual specimens available from contiguous areas within taxon localities. Specimens used for flavonoid analysis were selected as above, and on the basis of available (loose) leaf material. Material thus assembled is treated as representing populations. Herbarium specimens representing collections from Alaska, British Columbia, Alberta, Washington, Oregon, Idaho, Montana, Wyoming, Colorado, New Mexico, Utah, Nevada, Arizona and California were scrutinized. Specimens examined for this study are listed in Appendix I.

Tree characters recorded for samples include: habit and size of specimen; bark and

twig characteristics; health of specimen; presence of inflorescence or infructescence; fruit; proportion and location of heterophyllous leaves. Leaf characters recorded include abaxial and adaxial surface colour and vein architecture. Sites were characterized by geographic location, elevation, aspect, exposure, associated vegetation, proximity to water source and edaphic conditions.

Table 2.1.1. Collection Data¹

collection number	taxon locality	location	elevation
*†D1	douglasii	Interstate 90, opposite Lake Coeur d'Alene, Kootenai County, Idaho.	1000 m
†D2	douglasii	Highway 20, pull-off opposite Pass Lake, Deception Pass, Skagit County, Washington.	100 m
D3	douglasii	Highway 26, near mile 74, Mt. Hood National Forest, Wasco County, Oregon.	1700 m
D4	douglasii	Escarpment opposite VIA Rail Station, Prince Rupert, British Columbia.	10 m
F1	diffusum	Various sites in Charleston Mtns., Clark County Nevada	2500 m
F2	diffusum	Various sites in Spring Mtns., Clark County Nevada	2500 m
F3	diffusum	Various sites in the Snake Range, White Pine County Nevada	2500 m
F4	diffusum	Inyo County, California	2500 m
*G1	glabrum	Highway 119, above parking lot opposite Boulder Canyon Park, Boulder County, Colorado.	2000 m
†G2	glabrum	Highway 285 at Shawnee (between Grant and Bailey), Park County, Colorado.	2500 m
†G3	glabrum	Near summit of Bill Williams Mountain (near Flagstaff), Coconino County, Arizona.	2500 m
*†N1	neomexicanum	Highway 475, outside Hyde Memorial State Park, above Santa Fe, Santa Fe County, New Mexico.	2500 m
*†N2	neomexicanum	Highway 536, near Sandia Peak, above Placitas, Bernalillo County, New Mexico.	2000 m

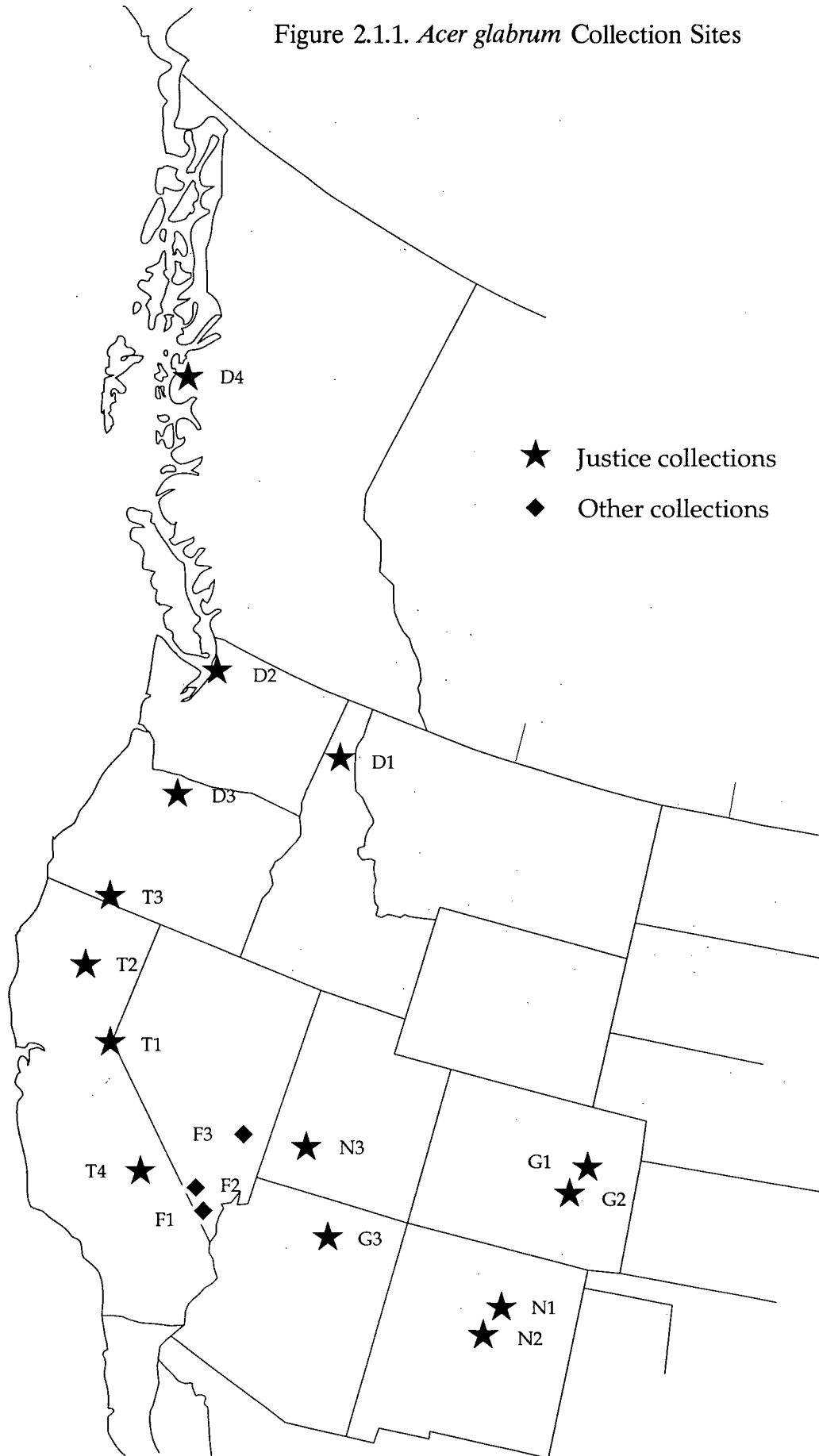
*†N3	neomexicanum	Hwy 14, ca. 16 km east of Cedar City, Iron County, Utah.	2000 m
*Nk	neomexicanum	El Porvenir (ca. 32 km west of Las Vegas), San Miguel County, New Mexico.	2800 m
*†T1	torreyi	Highway 50, northeast slope, above Lake Tahoe, Douglas County, Nevada.	2000 m
*†T2	torreyi	Highway 89, adjacent to Bluff Falls (Between Mineral and Lassen gate), Tehama County, California.	2500 m
*†T3	siskiyouense	Below ski hill; northeast slope of Mount Ashland, Jackson County, Oregon.	2500 m
*†T4	greenei	Road to Mineral King, Tulare County, California.	2000 m

¹ Material from all populations except F4 and Nk was used in morphometric analysis; material from all populations except F1, F2, F3 and Nk was used in flavonoid analysis.

* Seed also collected.

† Scions also collected.

Figure 2.1.1. *Acer glabrum* Collection Sites



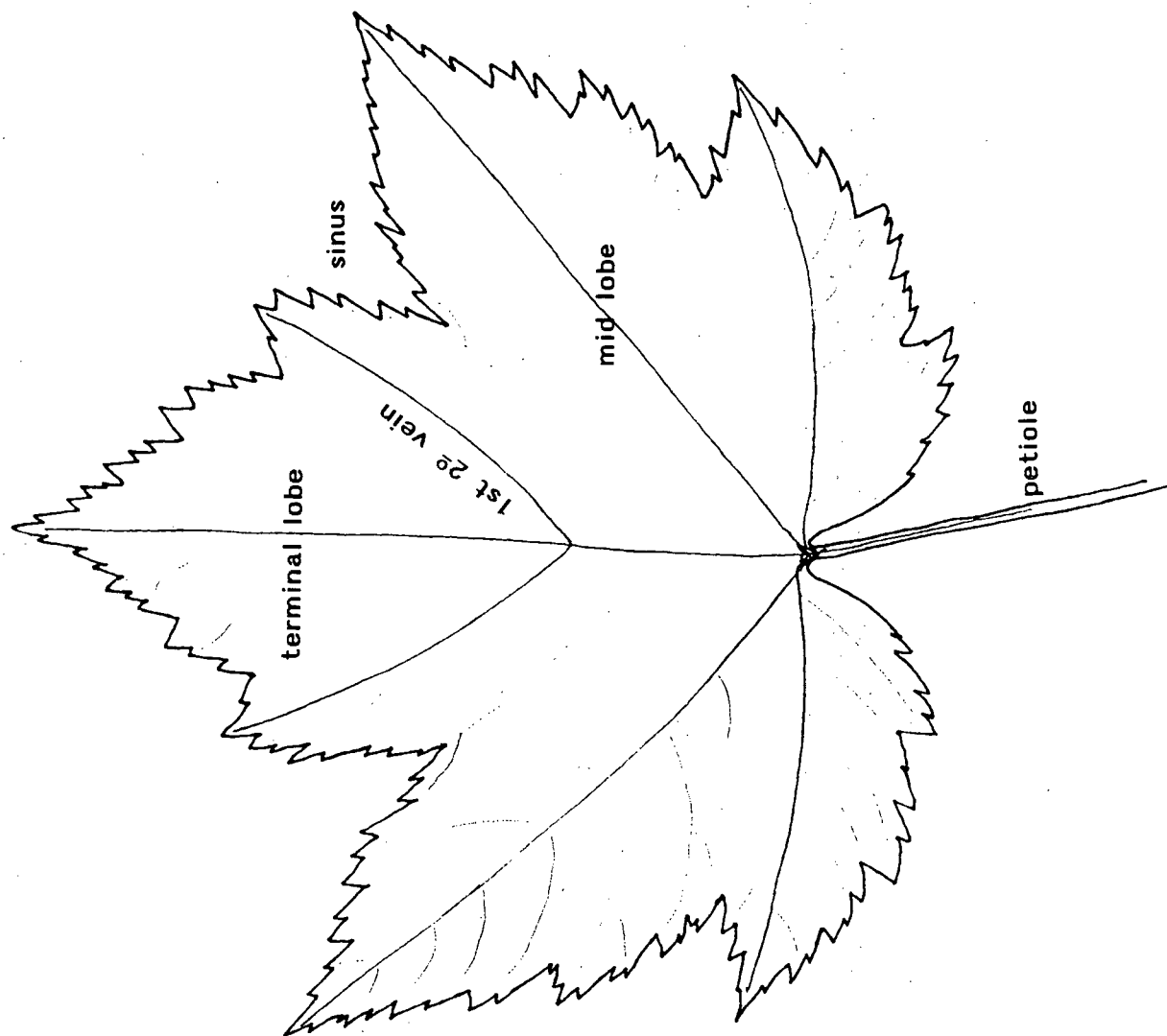
2.2. Morphometric Analysis

Dried leaves from collections and herbarium specimens (Table 2.1.1.) were characterized as arising from extension growth (E leaves) (internode length greater than 2 mm) or non-extension growth (N leaves) (internode length less than 2 mm). Extension and non-extension leaf categories are conceptually similar to those ascribed to seasonally heterophyllous leaves (i.e., neoformed or "late" leaves and preformed or "early" leaves, respectively) (Steingraeber, 1982). The former, less strict classification was employed here because determination of the developmental history of individual leaves was beyond the scope of this study.

Leaves were photocopied (photocopies of individual leaves are 1:1 two-dimensional reproductions) and the images manually measured for 8 linear and 2 count variables (Figure 2.2.1.). After photocopying, leaves were stored for subsequent flavonoid extraction (see below). Morphometric data for individual leaves were entered on Systat-MacIntosh, version 2.1.2. A total of 1537 leaves (cases) was entered, representing 141 trees, 17 populations and 7 taxon localities. Patterns of leaf variation for trees, populations and taxa were examined by principal components analysis (PCA; Sneath and Sokal, 1973), cluster and bivariate analyses.

Figure 2.2.1. Variables for Morphometric Analysis

Variables (distance in mm)	
LOB	= number of 1° veins
TTL	= length of the terminal lobe above 1st 2° vein terminating above sinus
BTL	= length of terminal lobe below 1st 2° vein terminating above sinus
TL1	= width of terminal lobe at deepest point in sinus
TL2	= width of terminal lobe at tooth terminating 1st 2° vein terminating above sinus
SEC	= length of 1st 2° vein terminating above sinus
SS	= length between petiole and deepest point in sinus
ML	= length of mid-lobe
TTH	= number of teeth on right side of terminal lobe
TSZ	= size of tooth terminating 1st 2° vein terminating above sinus



2.3. Transplant Studies

Seeds from 1993 collections were stratified in moist peat moss at approximately 0° C for 100 days, following the methods described by Schopmeyer (1974) and Folkerts (1994, pers. comm.), and subsequently planted in February 1994 in commercial potting media. Pots with seeds were grown either in a growth chamber (8-10 hours light per day, 5-8 degrees C. night temperature, 12-15 degrees C. daytime temperature) or unprotected, i.e., subjected to all incident weather conditions for UBC. No germination occurred for seeds in the growth chamber, so they were not included in this study. Seedlings from the 1992 collection of *P. Kelaidis* were planted in commercial nursery seedling media under a poly-tunnel at Mosterman Plant Propagators (Sardis, B.C.). Poly-tunnel conditions here are characterized by temperatures substantially in excess of ambient (outside) temperatures, approximately 10% shade, and automatic irrigation.

Collected scions were grafted on *Acer rubrum* L. and *A. davidii* Franchet seedling rootstocks in approximately equal numbers in February 1994 at Sardis. All grafted plants were held in propagation facilities at Sardis (bottom heat and frost protection) until bud-break. Surviving grafted plants were placed in the poly-tunnel housing the 1992 seedlings. All grafts and seedlings were observed in May 1994 and September 1994, and their leaf characteristics recorded.

2.4. Flavonoid Analysis

Samples used in flavonoid analysis were from collections noted above (Table 2.1.1.) and from herbarium specimens on loan to UBC (Inyo County California: F401 (DeDecker 2972); F402 (Munz 14850)) from the Jepson Herbarium (University of California, Berkeley). Individuals within collection areas (D206, D207; N205, N209; T402, T408), between different geographical populations (D105, D206, F401, F402, G210, N203, T205, T408), and a pooled sample consisting of leaves from all populations, were analyzed.

Isolation and identification of flavonoids

Dried leaf samples were extracted with 80% aq. methanol. Extracts of each sample were then treated as described by Wilkins and Bohm (1976) and subjected to two-dimensional TLC on Polyamid DC 6.6 plates. After air drying, the plates were sprayed with 0.1% diphenylboric acid ethanolamine complex (Naturstoffreagent A) in 1:1 methanol-water and allowed to stand for 1 h for colour development. The plates were then examined under UV light (366 nm) and scored for flavonoids. No discernable inter- or intra-population differences were visible, so extracts were combined to afford a greater working volume. Flavonoids were isolated using CC on Sephadex LH20 and purified using TLC according to Gornall and Bohm (1980). Extracts from combined samples were also subjected to two-dimensional descending chromatography according to the methods of Mabry *et al.* (1970). After air drying the chromatograms were treated as per visualization methods for Polyamid plates above and scored for flavonoids.

Flavonoids were isolated from spots and eluted with absolute methanol. Structures were

established using standard UV (Mabry *et al.*, 1970) and MS methods (Markham, 1982).

Purified glycosidic compounds were subjected to total and partial acid hydrolysis using methods described by Ceska and Stiles (1984) and Kartnig and Wegschaider (1971).

Isolated compounds agreed with standards available in our laboratory.

3.1. Field and Herbarium Studies

Selected samples (leaves and branches) from individual trees were mounted as herbarium specimens and deposited at UBC. Herbarium specimen labels showing field data for each of the populations collected are shown in Appendix II.

Field and herbarium study of *A. glabrum* var. *greeni* showed that populations of this taxon do not uniformly consist of plants with the supposedly distinguishing fruit character of the taxon. Rather, populations consist of intermixed individuals, some of which are typical *A. glabrum* var. *torreyi*, while others show varying degrees of samara wing overlap. Overlapping samara wings are also found in other *A. glabrum* infraspecific taxa. "Variety *greeni*" represents extreme forms in polymorphic populations. They are a polymorphism within populations, but do not form discrete populations, and are therefore not given infraspecific status in this paper (see Table 3.1.1. for list of collections with overlapping samara wings).

Similarly, observations of *A. glabrum* subsp. *siskiyouense* showed that populations of this taxon are not comprised of plants which all exhibit the supposedly distinguishing rhombic leaf lobe character. Populations consist of variable individuals, some of which are typical *A. glabrum* var. *torreyi*, while others show varying degrees of rhombic lobing. Rhombic lobes are also not restricted to the type locality of *A. glabrum* subsp. *siskiyouense*, the Siskiyou Mountains, but are found scattered throughout populations of varieties *torreyi*, *diffusum* and *neomexicanum*. "Subspecies *siskiyouense*" represents extreme forms in the normal range of leaf shape variability. These forms are a polymorphism within populations, but do not constitute discrete populations, and are therefore

Table 3.1.1. Collections with Overlapping Samara Wings

Taxon	Locality	Collection
<i>torreyi</i> (<i>greenei</i>)	Tulare County, California	Justice 028 (UBC)
<i>torreyi</i> (<i>greenei</i>)	Tulare County, California	Ferris & Lorraine 10663 (JEPS)
<i>torreyi</i> (<i>greenei</i>)	Tulare County, California	Rice 308 (UC)
<i>diffusum</i>	Inyo County, California	Thorne 56714 (UTC)
<i>diffusum</i>	San Bernardino County, CA	Munz 10778 (UC)
<i>diffusum</i>	Clark County, Nevada	T. Ackerman 1101 (UNLV)
<i>diffusum</i>	Clark County Nevada	Peterson 1428 (UNLV)
<i>diffusum</i>	Nye County, Nevada	Pinzl 2438 (NSMC)
<i>glabrum</i>	Coconino County, Arizona	Risk 2 (UNLV)
<i>douglasii</i>	Bannock County, Idaho	R. Wilson (1939) (U. of Idaho 46)

not given infraspecific status in this paper.

Field and herbarium study of *A. glabrum* var. *tripartitum* showed that not all plants in the type locality exhibit the supposedly distinguishing ternate leaf character. Populations consist of intermixed individuals, some of which show typical *A. glabrum* var. *glabrum* leaves, while others exhibit varying degrees of lobe division. The degree of lobe division present on any single tree or branch is presumably correlated with the timing and availability of soil moisture. "Variety *tripartitum*" represents the ternate-leaved extreme of the phenotypically plastic var. *glabrum*. These forms are *ecads*, i.e., their morphology determined by the environment from year to year, and are therefore not given infraspecific status in this paper.

All other infraspecific taxa, namely, varieties *diffusum*, *douglasii*, *glabrum*, *neomexicanum*, and *torreyi*, have relatively consistent distinguishing morphological characters that are correlated with more or less discrete geographical ranges. These characters intergrade to some degree where ranges overlap, showing a pattern typical of geographical varieties or subspecies in woody plants. The rest of this study is concentrated on the geographically distributed taxa.

Morphology

Leaf shape in Rocky Mountain maple varies according to geography. Leaves are largest in the north (var. *douglasii*), smallest in the intermountain region of the southwest (var. *diffusum*), most deeply divided in the southeast (var. *neomexicanum*), and bluntest in the southwest (varieties *diffusum* and *torreyi*). With a single exception, individual taxa can be characterized by the shapes of leaves that are initiated and partially developed in the season prior to their emergence; i.e., the defining leaf morphology for most taxa is expressed by early leaves. The exception, var. *neomexicanum*, produces late leaves precociously (compared with the other taxa), and late leaves represent the defining leaf morphology. Many of these intervarietal differences are supported by morphometric analyses, but qualitative characters (such as are listed below) are required for more thorough characterization of taxa.

Thickened, coriaceous leaves are most evident in taxa growing in areas with the highest summer temperatures and the least summer rainfall, and are thus most common in the varieties *diffusum* and *torreyi*. Vein architecture development is expressed to the highest degree in taxa exhibiting large leaves (varieties *neomexicanum* and especially

douglasii), and becomes more irregular and less developed as leaf size decreases.

Where intraspecific taxon ranges overlap, there is often wide variation in leaf shapes, from that typical of each taxon to intermediate forms, suggesting there is introgression among the taxa. The patterns of introgression are, however, somewhat confused by the inherent phenotypic plasticity exhibited by each of the taxa. Within taxa, leaf shape plasticity in early leaves is characterized primarily by variation in size, which appears to be displayed as a consequence of both spatial and temporal moisture availability.

Regardless of habitat locality, leaves initiated and fully developed in a single season often approach the morphology of var. *neomexicanum*; i.e., most late leaves are ternate or nearly so. There does not appear to be significant phenotypic plasticity with respect to late leaves, and differences in overall late leaf size are restricted to intervarietal variation. Late leaves are more prevalent in areas that receive moisture during warm summer temperatures, and thus are most common in the varieties *glabrum* and *neomexicanum*. Their distinctiveness is, to a great degree, due to growing season duration. Where growth is more or less continuous through a long growing season, few early leaves are preformed, and those are often small and rapidly succeeded by ternate or deeply divided late leaves. The time between cessation of growth and onset of winter dormancy is likely insufficient for the preformation of more than a small number of leaves. Hence, most leaves on shoots are ternate or deeply divided. In areas where growth is restricted by a lack of moisture, more preformed leaves are produced, and these leaves are less divided.

Most infraspecific taxa are distinguished by a small number of conspicuous leaf characters (Table 3.1.2.). Only the varieties *glabrum* and *torreyi* are superficially mor-

phologically similar. The majority of individuals observed both in the field and in herbarium specimens exhibit leaves of comparable size and basic shape. It is often necessary to use differences in vein architecture and leaf texture to distinguish the 2 taxa from herbarium specimens.

Table 3.1.2. Typical Leaf Characters for *A. glabrum* Intraspecific Taxa

taxon	typical leaf characters					
	width	sinus	teeth	abaxial surface	vein architecture* (Fig. 4.1.1.)	areole development* (Fig. 4.1.1.)
<i>diffusum</i>	<3 cm	variable (Fig. 5.3.5.)	small & blunt (Fig. 5.3.5.)	± coriaceous, scaberulose	3° barely visible	not visible
<i>douglasii</i>	8-18 cm	wide & shallow (Fig. 5.3.12.)	large & acute (Fig. 5.3.12.)	glabrous to glaucescent	5° visible, 4° orthogonal	good
<i>glabrum</i>	4-6 cm	moderate to deep (Fig. 5.3.1.)	large & acute (Fig. 5.3.1.)	± glabrous	5° visible, 4° reticulate	good
<i>neomexicanum</i>	5-10 cm	wide & very deep (Fig. 5.3.8.)	large & acute (Fig. 5.3.8.)	glauous	5° visible, 4° orthogonal	good
<i>torreyi</i>	4-6 cm	narrow & deep (Fig. 5.3.9.)	moderate & blunt (Fig. 5.3.9.)	± coriaceous, smooth	4° visible, reticulate	poor

* Hickey (1973)

3.2. Morphometric Analysis

Bivariate Analysis

Taxon statistics were determined for all variables (Appendix III). All variable means were individually plotted to ascertain which showed distinctive intervarietal trends (Figure 3.2.1.) Taxon mean comparisons (Table 3.2.1.) were generated to determine whether mean differences were significant.

The variables LENGTH, TSIZE and SINUS appear to be the most robust for resolving taxa. The variable SS was recoded as: $1 - (SS / ML)$ to give SINUS (sinus depth as a proportion of midlobe length), and where SS equals 0, SS was recoded to equal 1 mm. LENGTH (overall length) was created by adding TTL and BTL.

These 3 independent variables were then plotted to determine whether they show trends with respect to taxonomic, populational and categorical environmental variables (Figures 3.2.2. to 3.2.8). Latitude (degrees N.) is primarily a measure of incident radiation, since light levels increase southward in western North America as a result of both reduction in cloud cover and increase in angle of incident sunlight. Summer temperatures are higher at lower latitudes, and although this is offset to some degree by the increase in habitat altitude, exposure to ultraviolet radiation — which contributes to heat-loading in leaves — intensifies with increasing altitude. Moisture availability is calculated as growing-season rainfall plus winter precipitation that accumulates as snow for that area. Values are based on published long-term averages.

Mean leaf length increases with latitude (northward) (Figure 3.2.2.a.) and increasing moisture availability (Figure 3.2.2.b.). This trend is mirrored to some degree by mean

Figure 3.2.1. Trends for Measured Variables

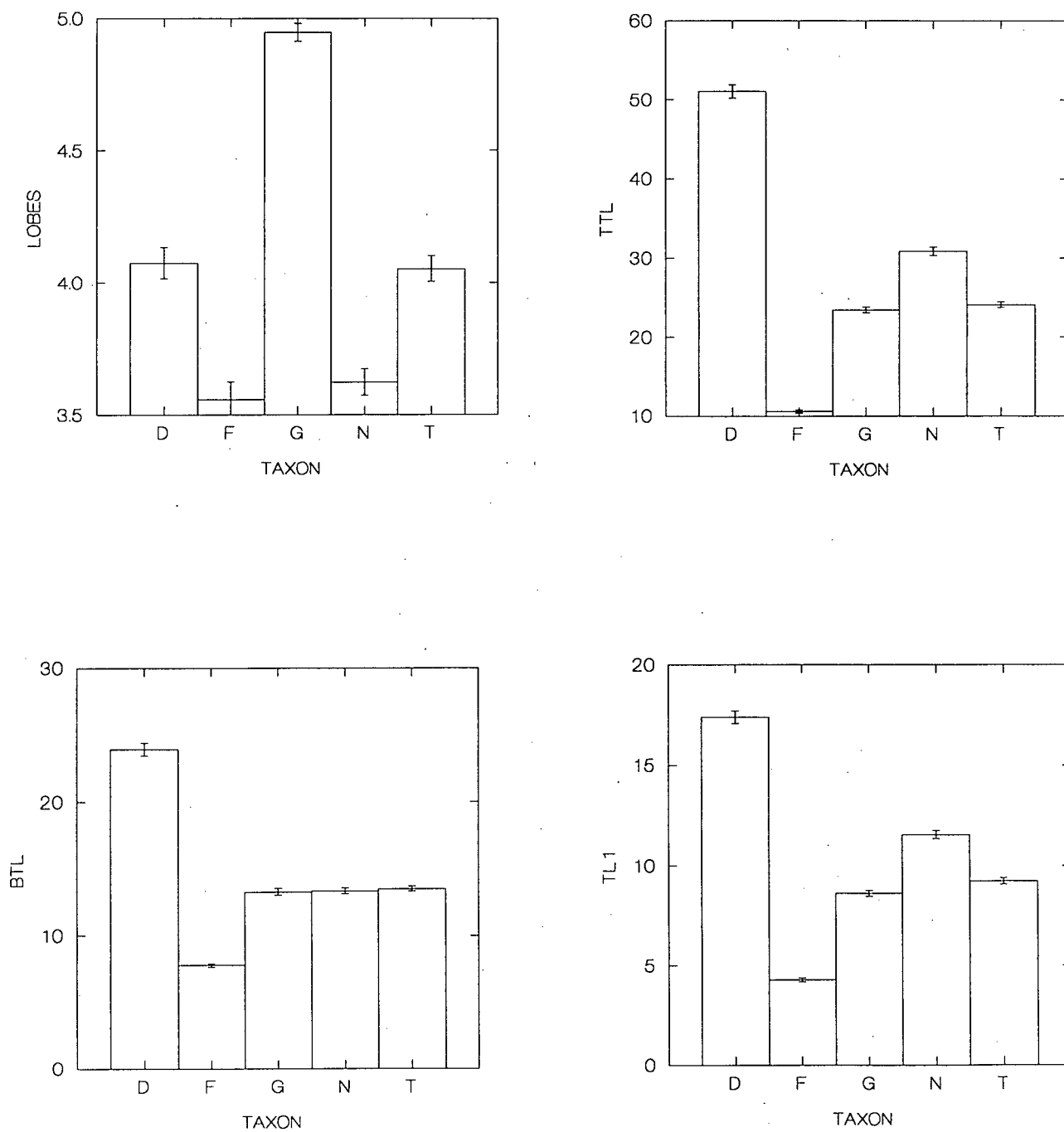


Figure 3.2.1. continued

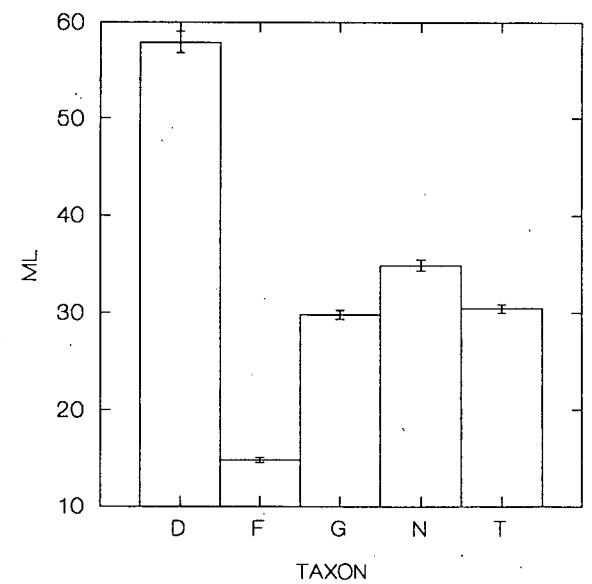
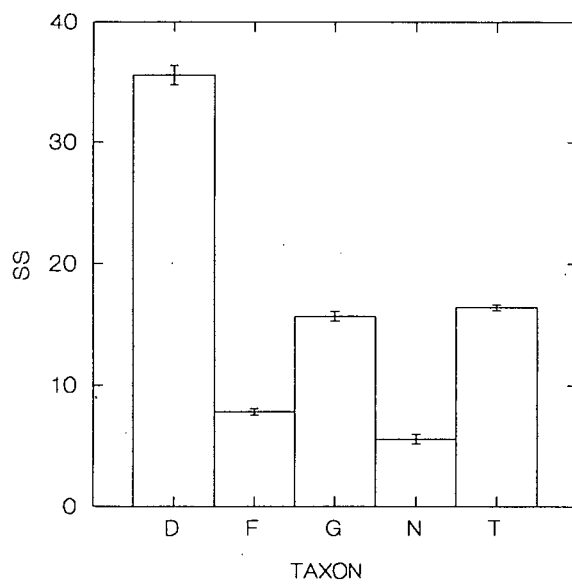
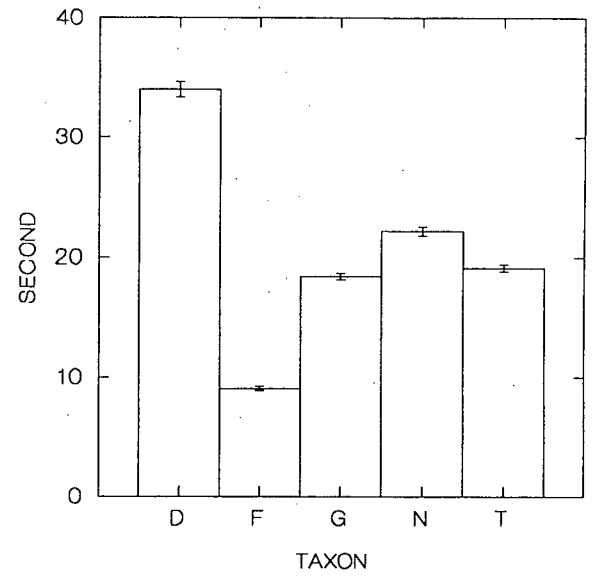
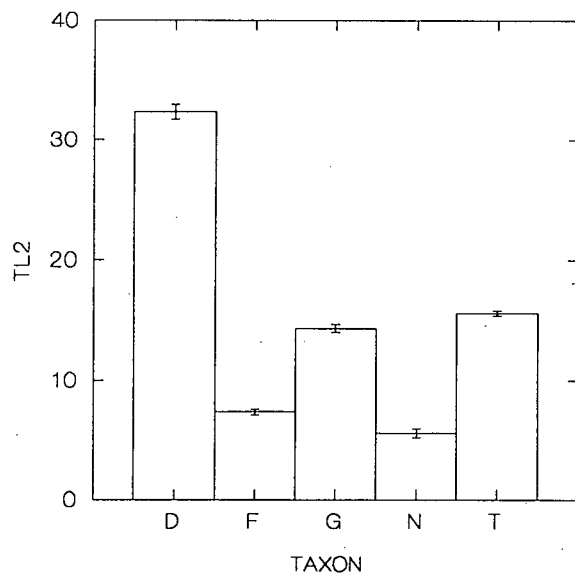


Figure 3.2.1. continued

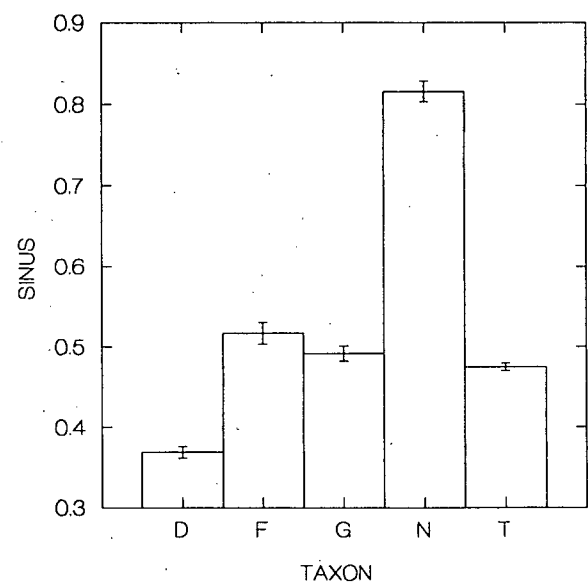
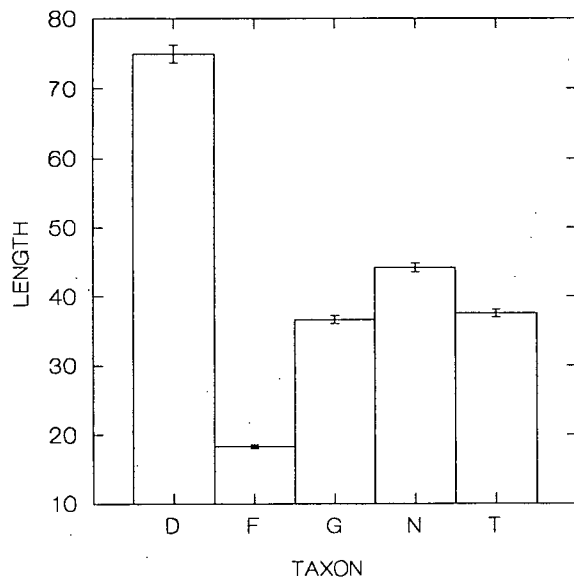
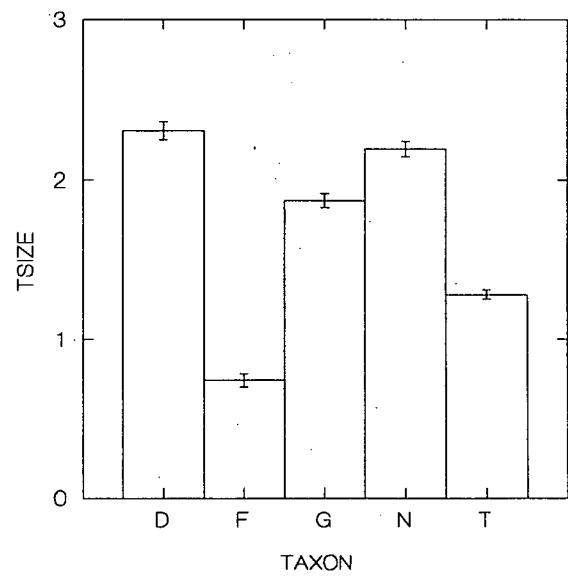
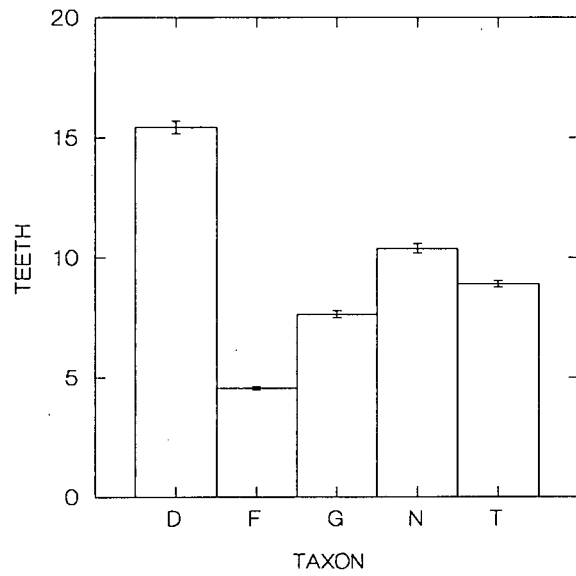


Table 3.2.1. Leaf Variable Taxon Mean Comparisons

Comp.*	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ	LEN	SIN
D x F	S	S	S	S	S	S	S	S	S	S	S	S
D x G	S	S	S	S	S	S	S	S	S	S	S	S
D x N	S	S	S	S	S	S	S	S	S	NS	S	S
D x T	NS	S	S	S	S	S	S	S	S	S	S	S
F x G	S	S	S	S	S	S	S	S	S	S	S	NS
F x N	NS	S	S	S	S	S	S	S	S	S	S	S
F x T	S	S	S	S	S	S	S	S	S	S	S	S
G x N	S	S	NS	S	S	S	S	S	S	S	S	S
G x T	S	NS	NS	NS	S	NS	NS	NS	S	S	NS	NS
N x T	S	S	NS	S	S	S	S	S	S	S	S	S

* D = var. *douglasii*; F = var. *diffusum*; G = var. *glabrum*; N = var. *neomexicanum*;
 T = var. *torreyi*

S = significantly different ($p < 0.05$)

NS = not significantly different ($p > 0.05$)

Figure 3.2.2. Mean Leaf Length by Environment

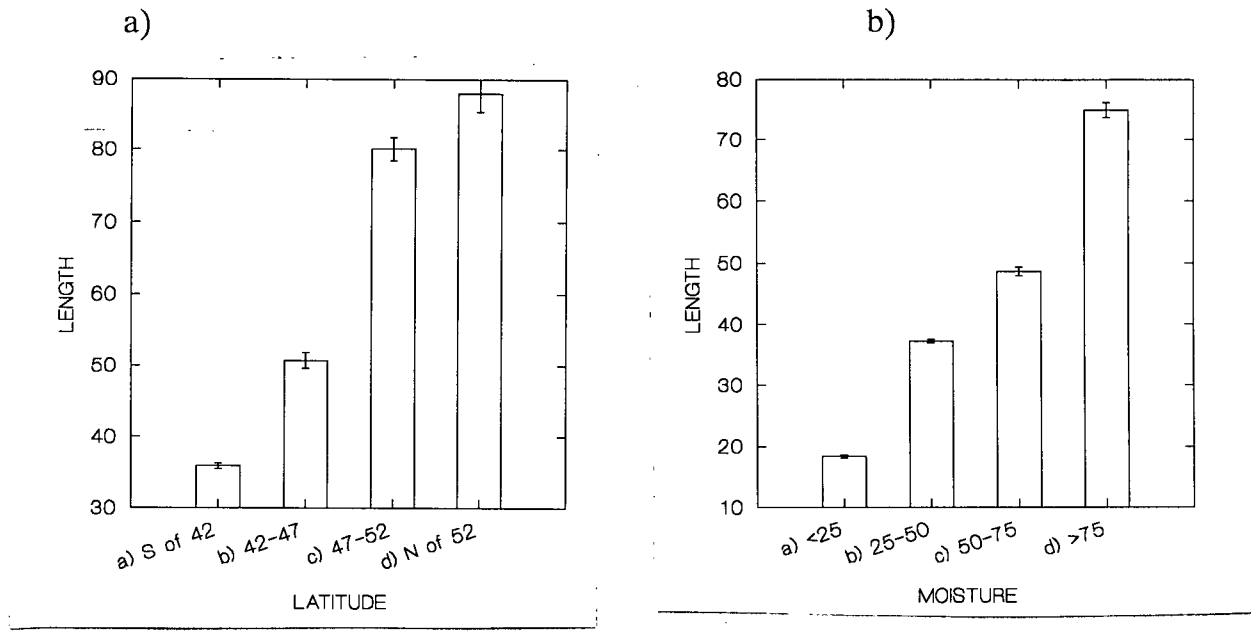


Figure 3.2.3. Mean Marginal Tooth Size by Environment

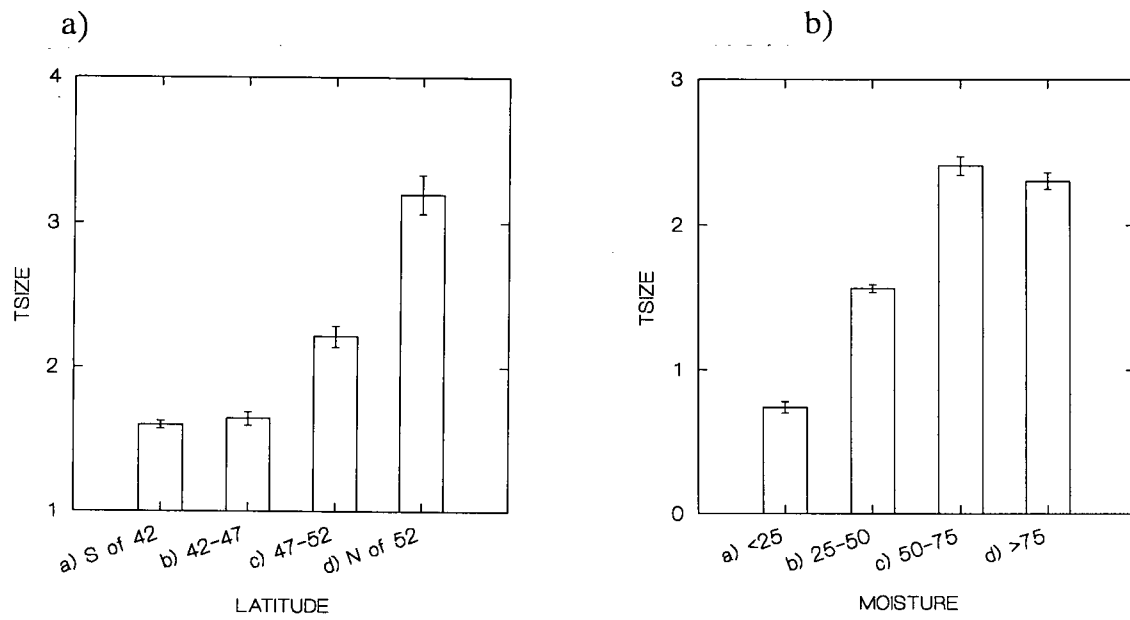


Figure 3.2.4. Mean Sinus Depth by Environment

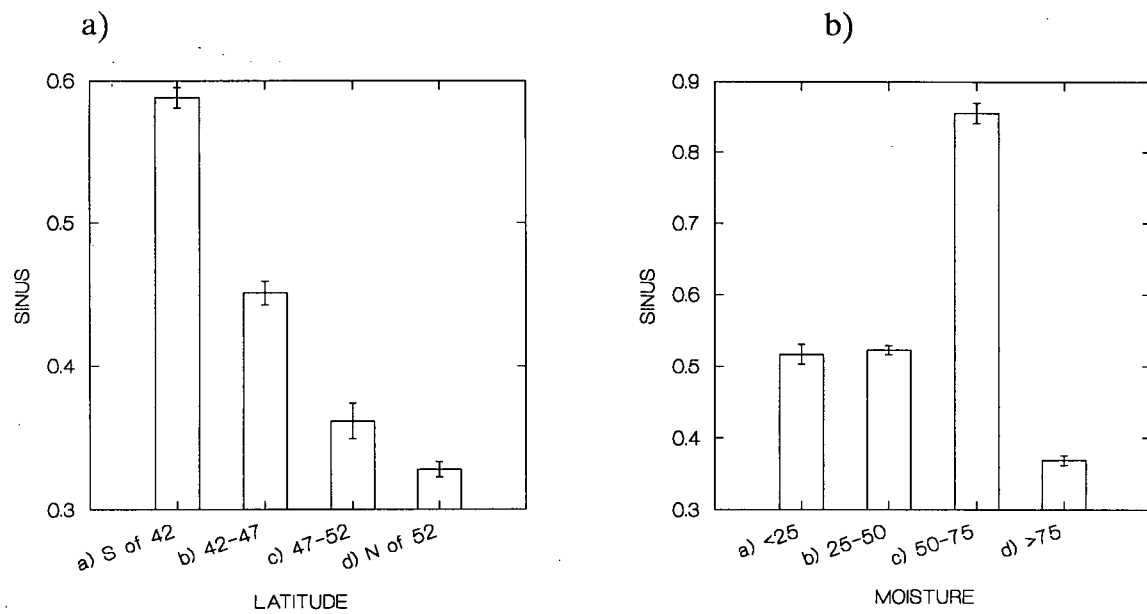


Figure 3.2.5. Mean Leaf Measurements by Population

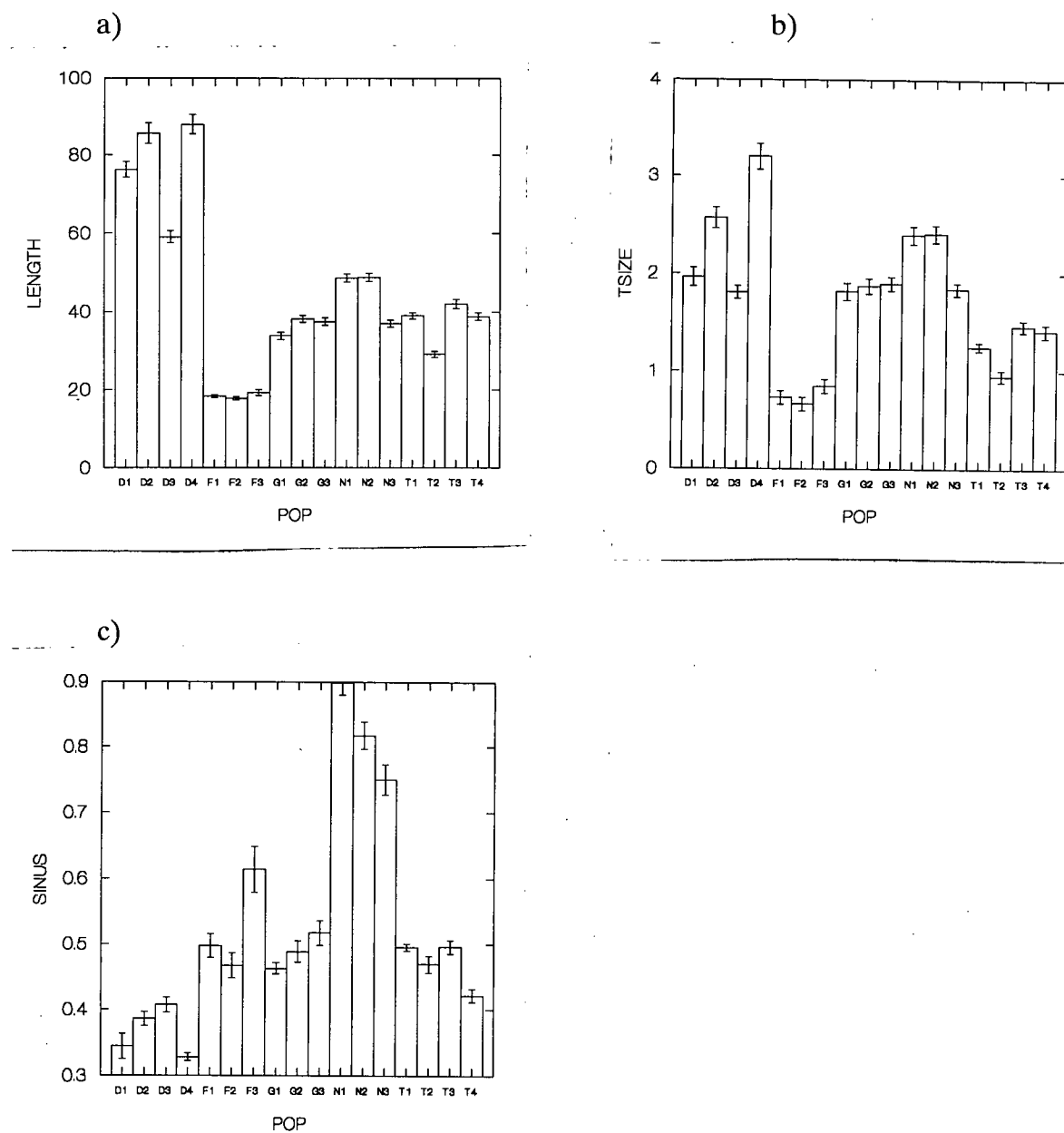
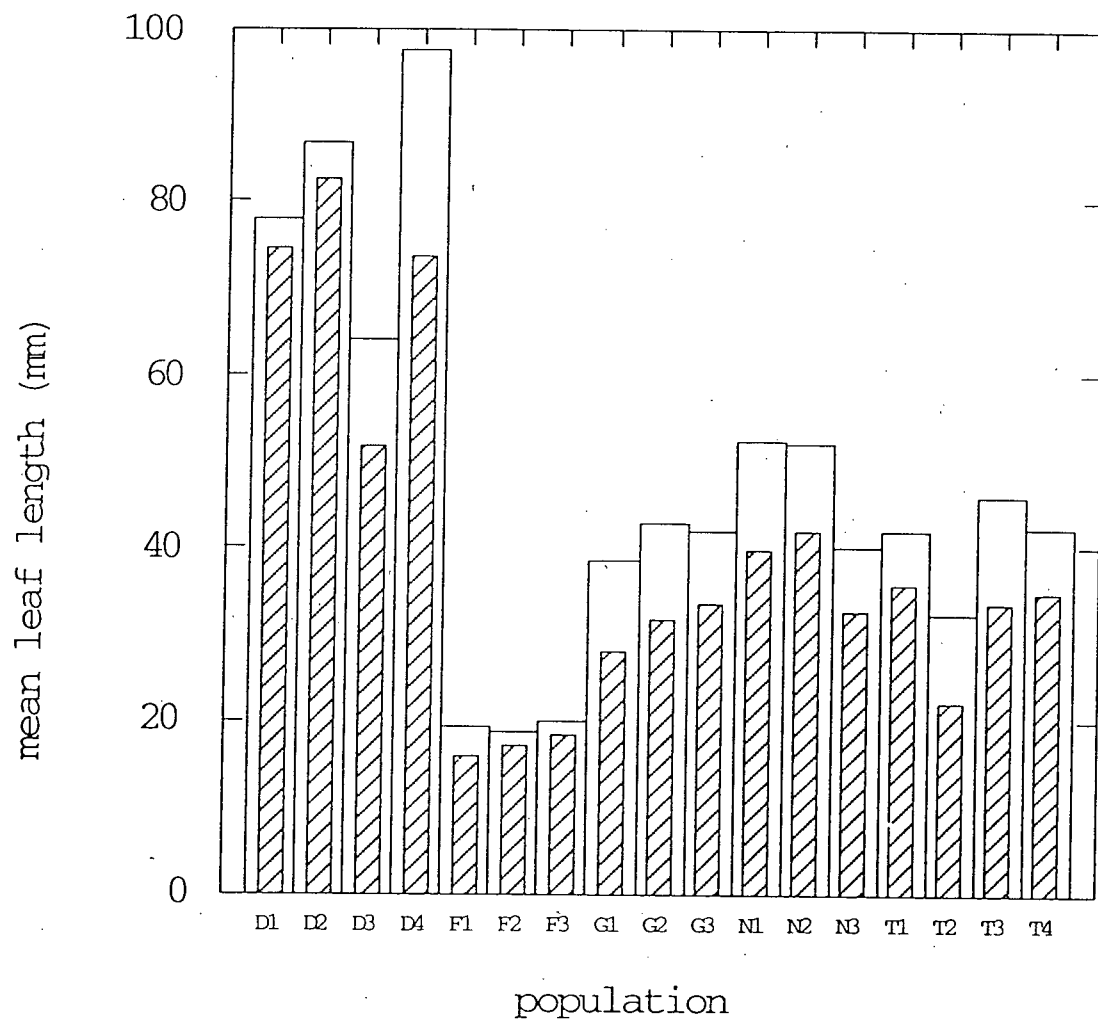


Figure 3.2.6. Mean Leaf Length for Leaf-types by Population



Extension Leaves



Non-Extension Leaves

Figure 3.2.7. Mean Sinus Depth for Leaf-types by Population

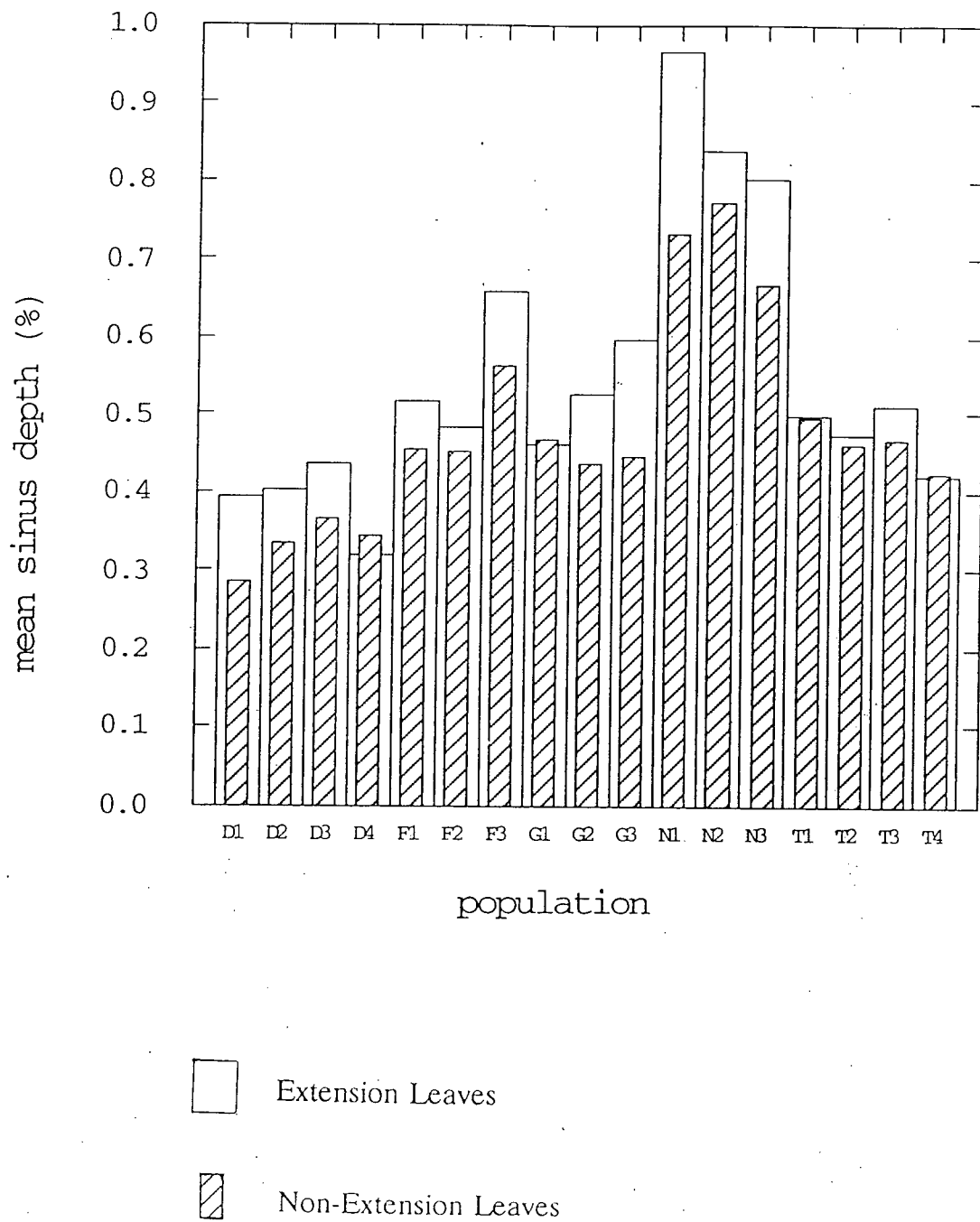
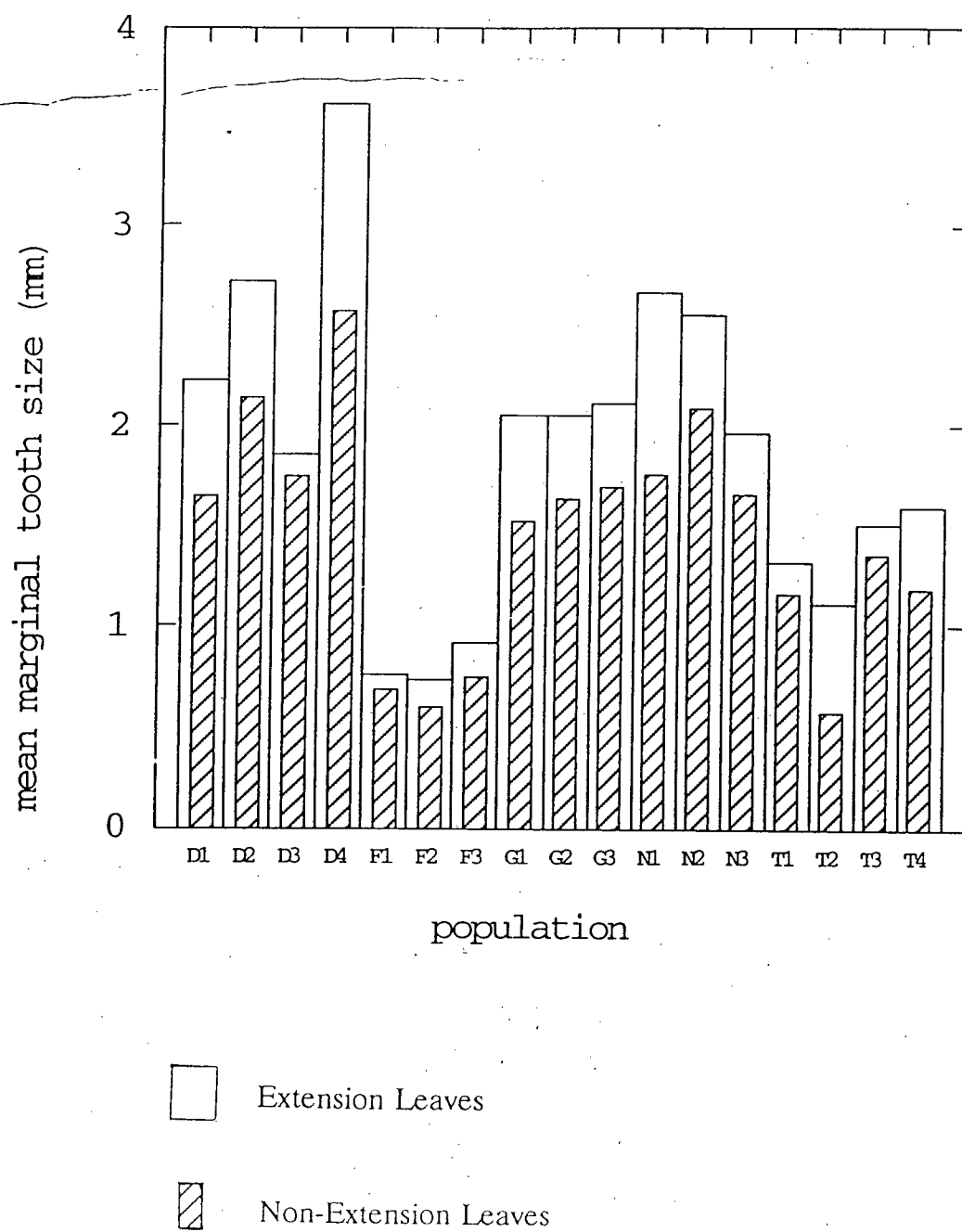


Figure 3.2.8. Mean Marginal Tooth Size for Leaf-types by Population



marginal tooth size (Figures 3.2.3.a. and 3.2.3.b.). The reverse is found for mean sinus depth (i.e., sinus depth increases southward) (Figure 3.2.4.a.). Moisture availability is correlated with increasing sinus depth, but only where annual precipitation is below 75 cm (Figure 3.2.4.b.).

Among populations, 3 relatively distinct groups, corresponding to varieties *douglasii* and *diffusum* and an assemblage that includes the remaining varieties, are resolved by mean leaf length (Figure 3.2.5.a.). Varieties *diffusum* and *torreyi* are discriminated by mean marginal tooth size among populations (Figure 3.2.5.b.). All other taxa are either variable among populations, or share average tooth size with other taxa. Only var. *neomexicanum* is distinctive among populations with respect to mean sinus depth (Figure 3.2.5.c.).

Extension (E) leaves are larger on average than non-extension (N) leaves for all populations (Figure 3.2.6.), and all taxa show significant size differences between extension and non-extension leaves (Table 3.2.2.). Extension leaves have deeper sinuses than non-extension leaves for most populations, and consistently deeper sinuses in varieties *neomexicanum* and *diffusum* (Figure 3.2.7.), but differences are not significant within varieties *douglasii* and *torreyi*. Marginal teeth are significantly larger on extension leaves of all taxa except var. *diffusum* (Table 3.2.2.; Figure 3.2.8.).

Principal Components Analysis

The shape of *Acer glabrum* leaves varies in many ways, including overall size, lobe number, lobe shape, sinus depth, and marginal toothings. Principal components analysis (PCA) performed on the 10 variables and 1537 cases of the *Acer glabrum* data set

Table 3.2.2. Variable Taxon Mean Comparisons for Leaf-types

TAXON	LENGTH	Tsize	SINUS
<i>douglasii</i> E × N leaves	S	S	NS
<i>diffusum</i> E × N leaves	S	NS	S
<i>glabrum</i> E × N leaves	S	S	S
<i>neomexicanum</i> E × N leaves	S	S	S
<i>torreyi</i> E × N leaves	S	S	NS

S = significantly different ($p < 0.05$)

NS = not significantly different ($p > 0.05$)

produced 2 meaningful eigenvalues or principal components (Table 3.2.3.). The 1st principal component describes 68.6 percent of the total variation inherent in the original variables, and the 2nd 12.3 percent. Component loadings (Table 3.2.3.) show the relative magnitude of each variable's contribution to the principal components. Here, the 1st principal component is primarily a measure of overall size, evinced by high positive loadings for all linear variables. Negative and positive correlations of both linear and count variables show that the 2nd principal component reflects both size and shape (although admittedly weakly).

Graphically, the 1st and 2nd principal components represent axes on a Cartesian plane (i.e., "x" and "y"), and provide each individual leaf a set of x,y coordinates. Scatter

Table 3.2.3. PCA Eigenvalues and Component Loadings

Latent Roots (Eigenvalues)									
1	2	3	4	5	6	7	8	9	10
6.857	1.228	0.815	0.559	0.248	0.142	0.072	0.034	0.027	0.019

Component Loadings

Variable	1st principal component	2nd principal component
LOB	0.175	-0.723
TTL	0.962	0.176
BTL	0.898	-0.137
TL1	0.933	0.199
TL2	0.811	-0.432
SEC	0.967	0.130
Ss	0.806	-0.455
ML	0.975	0.047
TTH	0.798	0.266
Tsz	0.627	0.363

Percent of Total Variance Explained by Components

1	2
68.570	12.278

plots and plots with *bivariate ellipses* around coordinate points are presented in Figures 3.2.9. to 3.2.12. (In some plots, coordinate points are omitted for clarity.) The major axes of a bivariate ellipse are determined by the unbiased sample standard deviations of x and y, and its orientation is determined by the sample covariance between x and y. A 95 percent confidence ellipse is defined such that there is 95 percent probability that the ellipse surrounds the mean value of a population for which the measured leaves are a sample.

Figure 3.2.9 shows coordinate points representing individual leaves in each infraspecific taxon. Although scatters exceed the confidence ellipses, the position, size and orientation of the ellipses reflects the taxon's overall tendency to vary. For example, the leaves of var. *diffusum* feature the smallest scatter and confidence ellipse, and therefore are the least variable leaves of all taxa. The greatest spread and largest confidence ellipse is exhibited by var. *douglasii*, demonstrating that it is the most variable taxon. The orientation and shape of var. *neomexicanum*'s ellipse establishes that it is comparatively variable, and that it is notably so in the factor 1 direction. Extension and non-extension leaves for each taxon are represented in plots presented in Figure 3.2.10. All taxa show ellipses for extension leaves with more positive x and y values than ellipses for non-extension leaves. In other words, extension leaves are larger and more "shapely" than non-extension leaves in all taxa. Only var. *neomexicanum* exhibits extension leaves less variable than non-extension leaves; all other taxa have similarly variable extension and non-extension leaves. Compared to all other taxa, the lesser relative overlap of leaf-type ellipses for varieties *glabrum* and *neomexicanum* suggest that extension and non-extension leaves are more distinct in these taxa, and independent t-tests (Table 3.2.6.)

Figure 3.2.9. PCA Taxon Scatter Plots

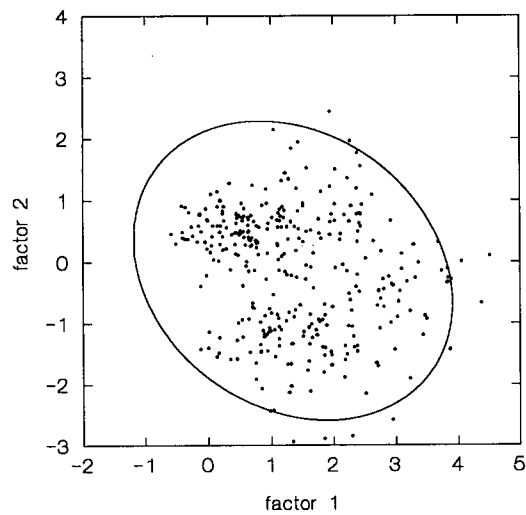
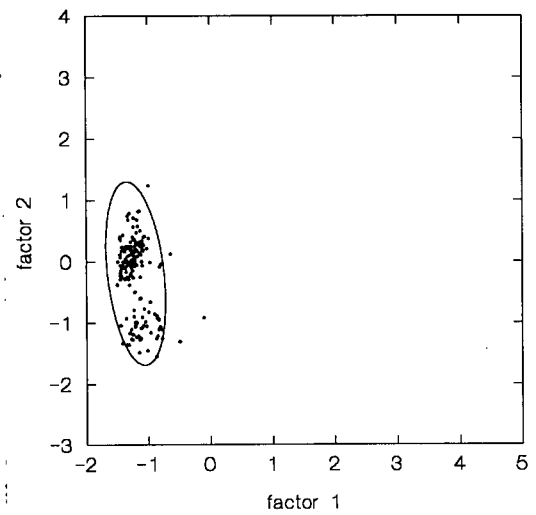
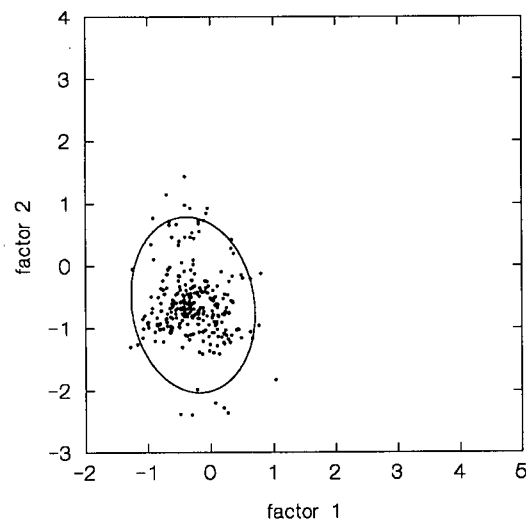
a) *var. douglasii*b) *var. diffusum*c) *var. glabrum*

Figure 3.2.9. continued

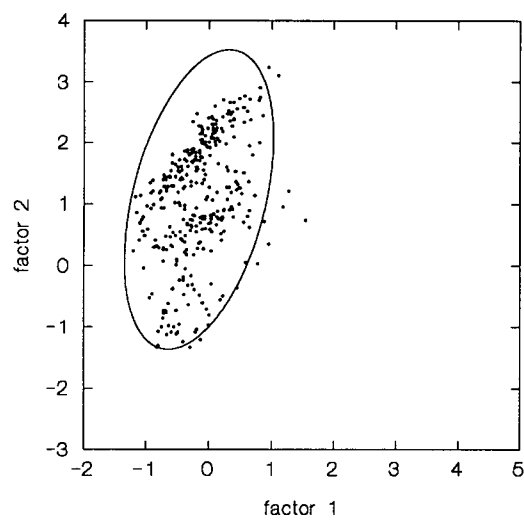
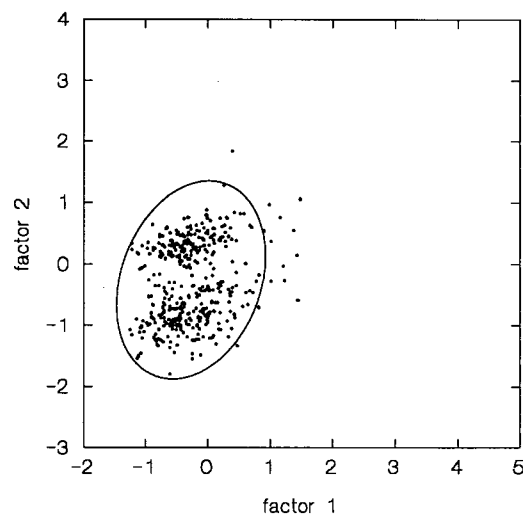
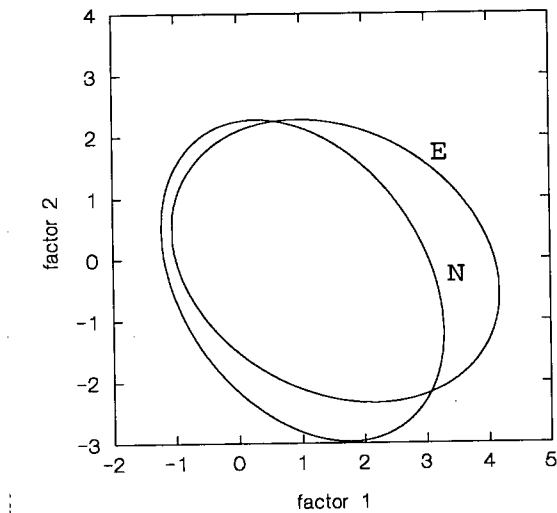
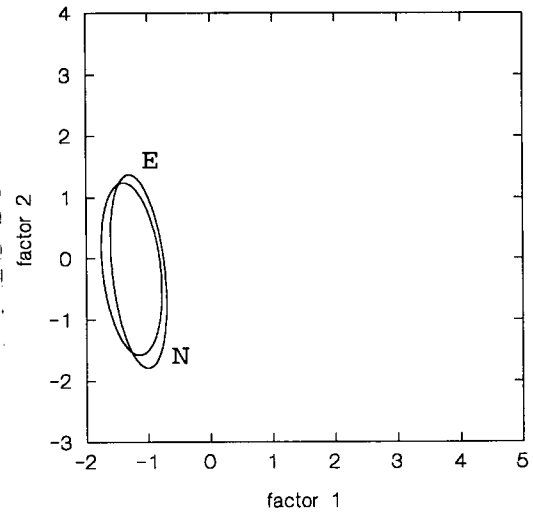
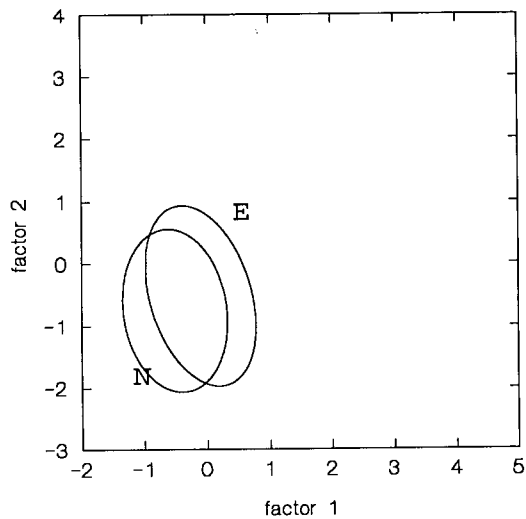
d) var. *neomexicanum*e) var. *torreyi*

Figure 3.2.10. PCA Taxon Plots for Leaf-types

a) *var. douglasii*b) *var. diffusum*c) *var. glabrum*

E = Extension Leaves

N = Non-extension Leaves

Figure 3.2.10. continued

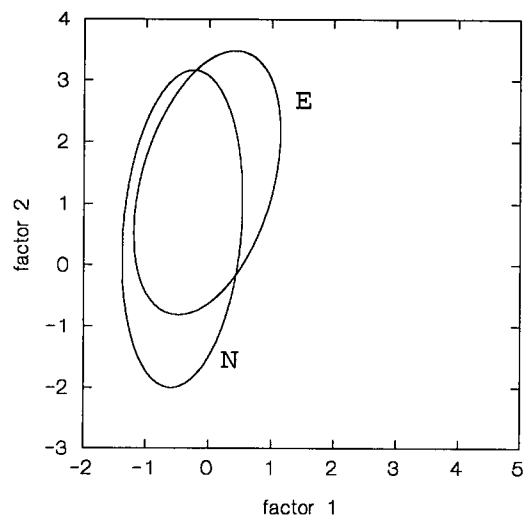
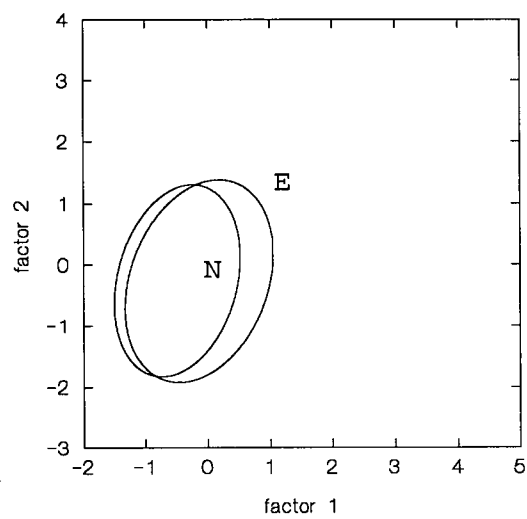
d) var. *neomexicanum*e) var. *torreyi*

Figure 3.2.11. PCA Population Plots

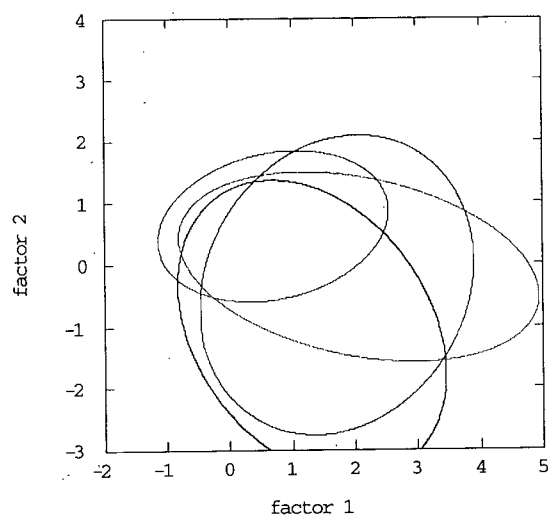
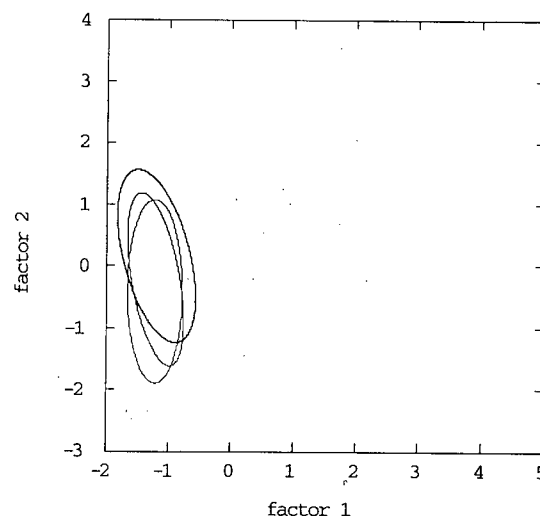
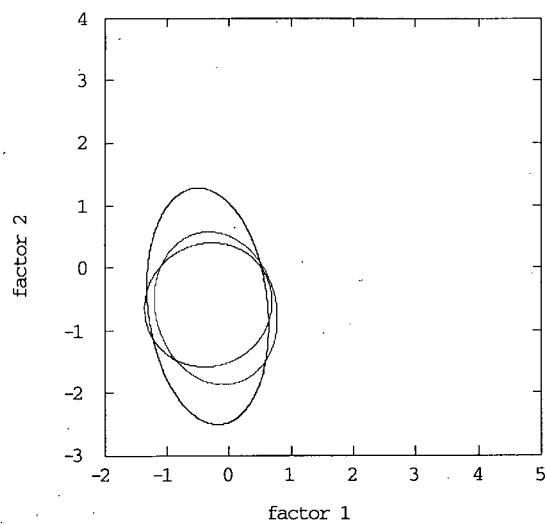
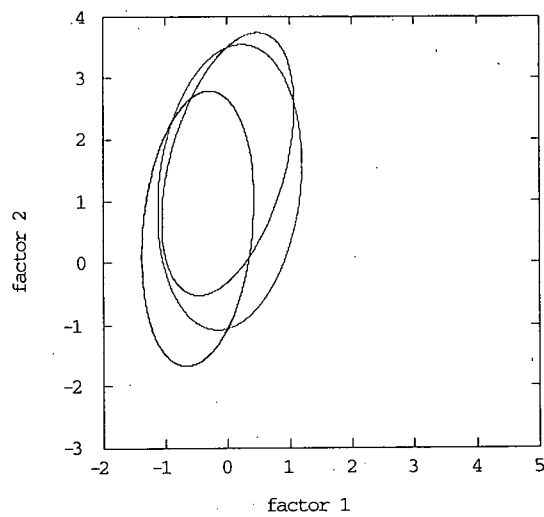
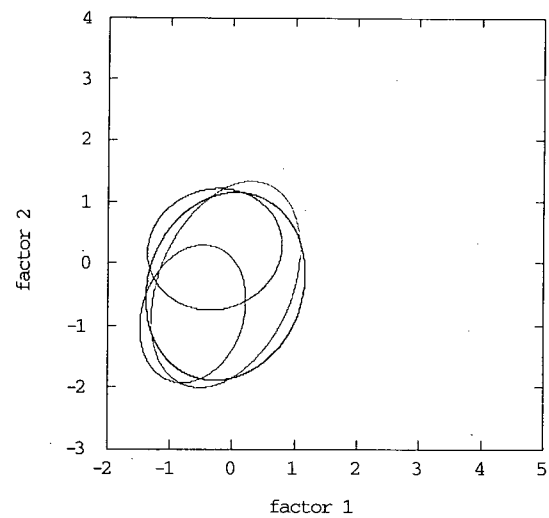
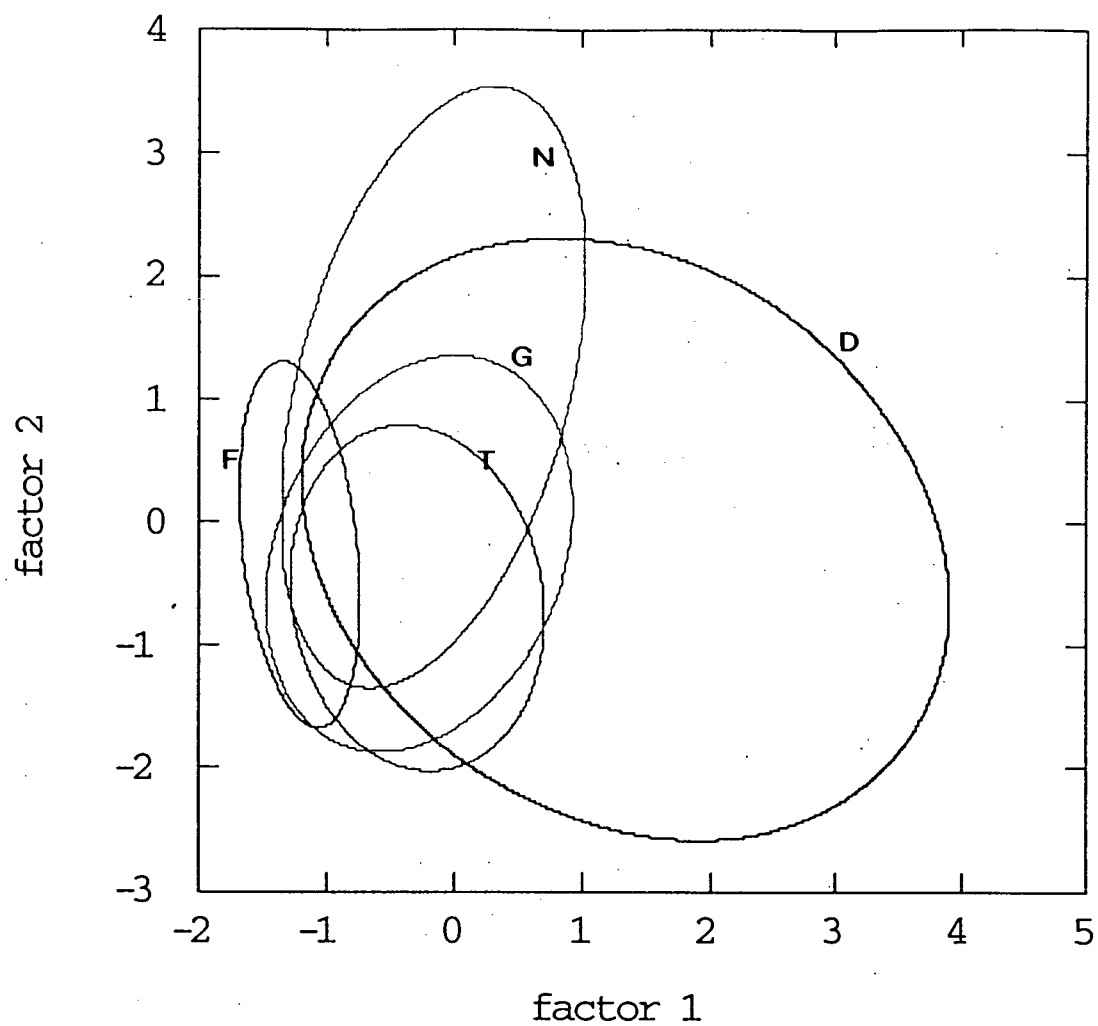
a) *var. douglasii*b) *var. diffusum*c) *var. glabrum*

Figure 3.2.11. continued

d) var. *neomexicanum*e) var. *torreyi*



D = var. *douglasii*; F = var. *diffusum*; G = var. *glabrum*; N = var. *neomexicanum*;

T = var. *torreyi*

Table 3.2.4. PCA Taxon Mean Comparisons for Leaf-types

Taxon	PCA1	PCA2
<i>douglasii</i> E × N leaves	S	NS
<i>diffusum</i> E × N leaves	S	NS
<i>glabrum</i> E × N leaves	S	S
<i>neomexicanum</i> E × N leaves	S	S
<i>torreyi</i> E × N leaves	S	NS

S = significantly different ($p < 0.05$)

NS = not significantly different ($p > 0.05$)

show that means are significantly different for both principal component axes in these 2 taxa.

Leaves from different populations for each taxon are represented in plots shown in Figure 3.2.11. The plot for var. *douglasii* shows that that taxon is highly variable, both among and within populations, whereas all other taxa are less variable in this respect. Population D3 (Figure 3.2.11.b.) represents the most southerly var. *douglasii* population collected in this study (northwest Oregon), and appears the least variable and most discrete of all var. *douglasii* populations.

Figure 3.2.12. is a plot showing confidence ellipses for the 5 infraspecific taxa accepted in this study. While there is considerable overlap of ellipses for all taxa, ellipses differ in size, position and orientation. Principal component taxon mean comparisons (Table 3.2.7.) show that only varieties *glabrum* and *torreyi* are not significantly different with respect to factor 1 means. PCA seems unable to resolve varieties *glabrum* and

Table 3.2.5. PCA Taxon Mean Comparisons for All Leaves

*Comp.	PCA1	PCA2
D x F	S	NS
D x G	S	S
D x N	S	S
D x T	S	NS
F x G	S	NS
F x N	NS	S
F x T	S	NS
G x N	S	S
G x T	NS	S
N x T	S	S

* D = var. *douglasii*; F = var. *diffusum*; G = var. *glabrum*; N = var. *neomexicanum*;
T = var. *torreyi*

S = significantly different ($p < 0.05$)

NS = not significantly different ($p > 0.05$)

torreyi, given the factor score coordinates ascribed to each.

Cluster Analysis

Population means for each of the 10 original variables were used to produce the cluster diagram in Figure 3.2.13. This cluster and those following are calculated using *Euclidean Distance* and *Average Linkage Method* (also known as UPGMA), a method that has received wide acceptance (Pimentel, 1993). Here, varieties *douglasii* and *glabrum* are

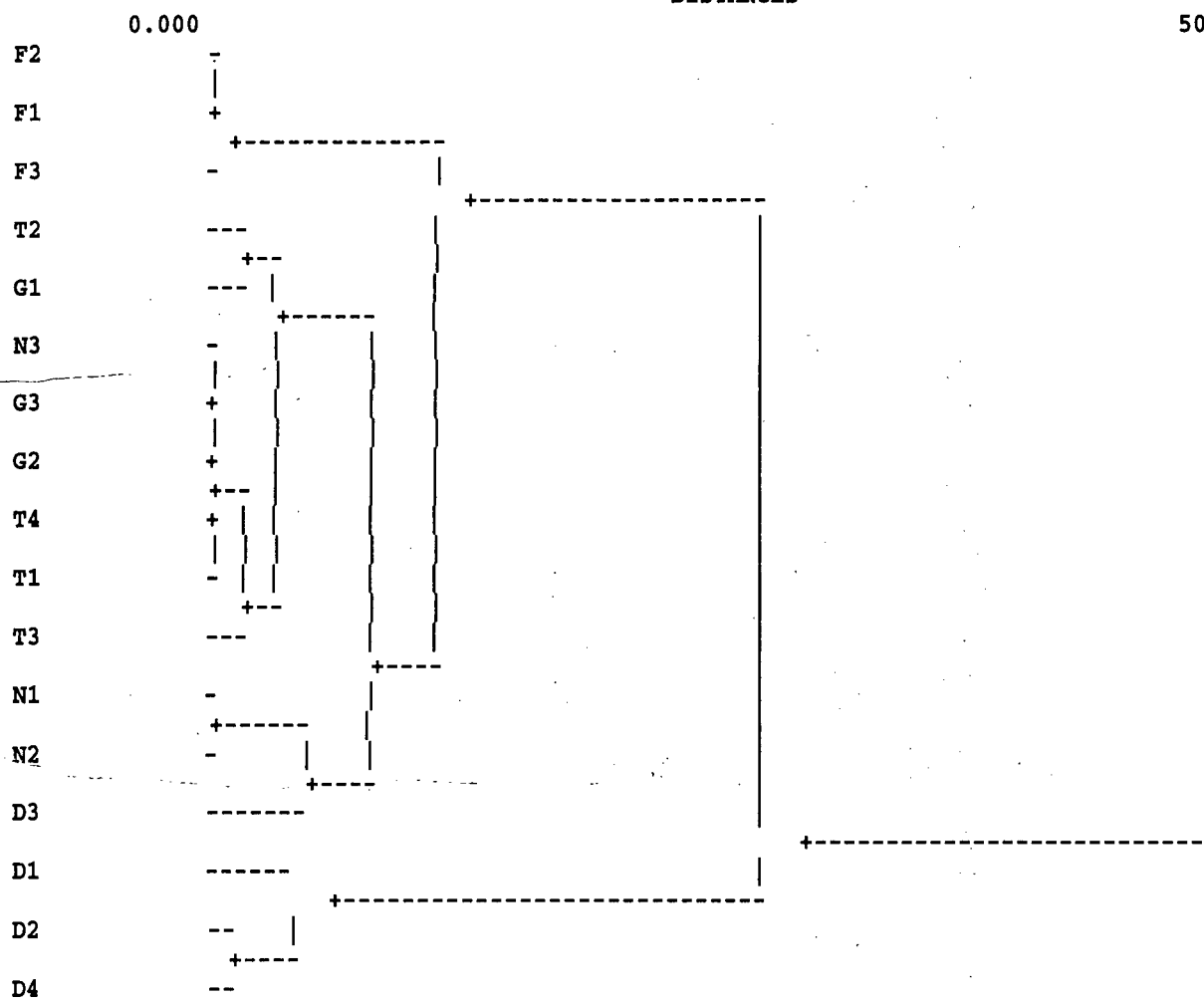
Figure 3.2.13. Cluster 1 - Measured Variables

DISTANCE METRIC IS EUCLIDEAN DISTANCE
AVERAGE LINKAGE METHOD

TREE DIAGRAM

DISTANCES

50



resolved, as are the varieties *diffusum* and *neomexicanum*. The cluster containing the populations of varieties *glabrum* and *torreyi*, however, shows that either individual populations are too similar among these taxa, or that overall, they are not different enough to warrant segregation. Figure 3.2.14. features a cluster diagram derived from population mean factor 1 and factor 2 scores. Again, populations of some taxa nest within other taxa, and overall, the picture is confusing. As with the PCA scatter plots, resolution of taxa is hampered by the overwhelming influence of size variables on the analysis.

Variables that vary profoundly, but which are represented by numerically small values (e.g., marginal tooth size) are swamped by those represented by numerically large values in these analyses. To offset this effect, log transformation was used on all continuous variables. The cluster diagram produced (Figure 3.1.15.) shows all populations (with a single exception) grouping within their ascribed taxa. The cluster diagram in Figure 3.2.16. uses vein architecture, areole development and log-transformed variables. Here, presumably because of the inclusion of categorical variables, together with variables where the size component has been discounted, all infraspecific taxa are completely resolved.

Figure 3.2.14. Cluster 2 - PCA Factors

DISTANCE METRIC IS EUCLIDEAN DISTANCE
AVERAGE LINKAGE METHOD

TREE DIAGRAM

DISTANCES

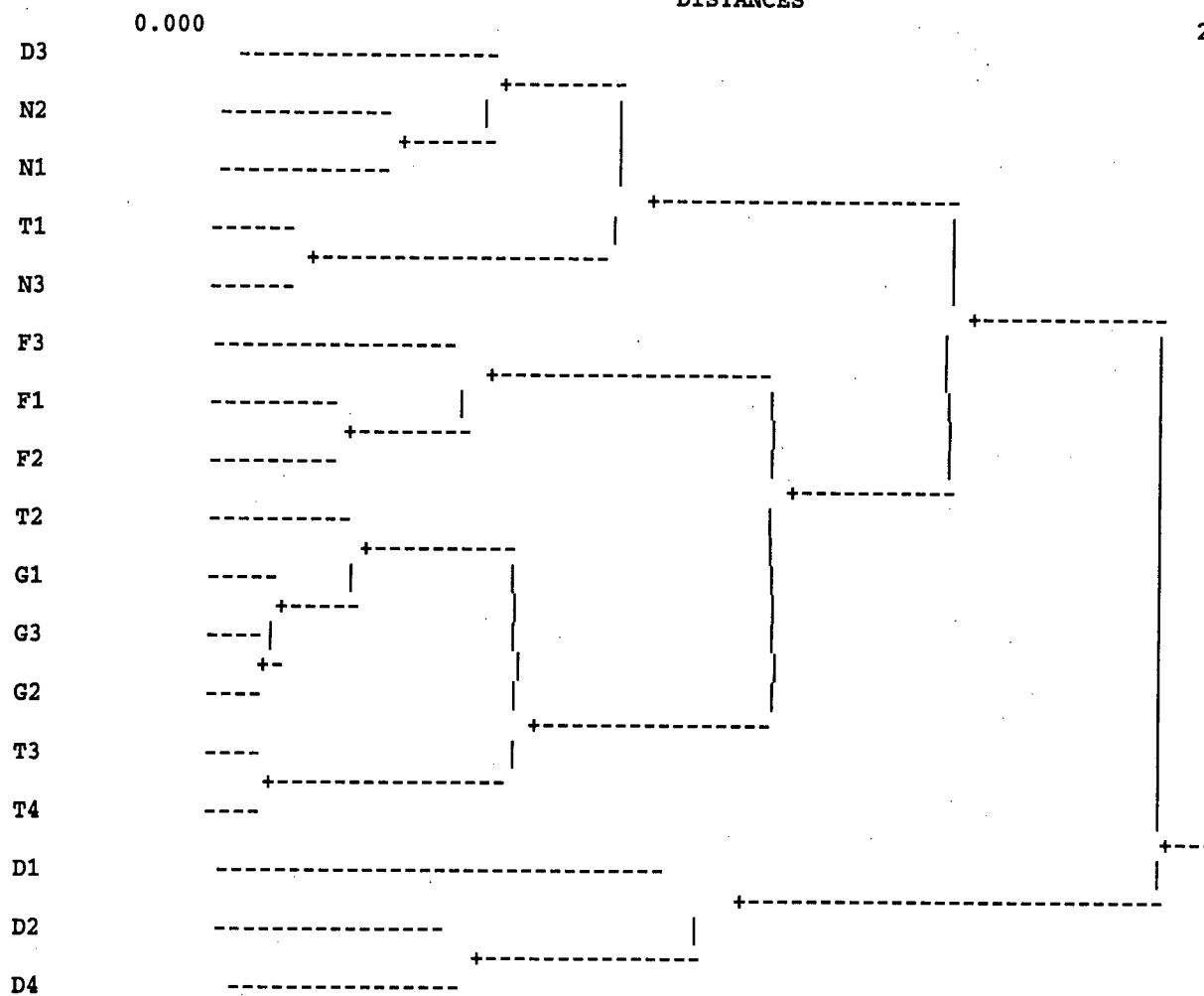


Figure 3.2.15. Cluster 3 - Transformed Measured Variables

DISTANCE METRIC IS EUCLIDEAN DISTANCE
AVERAGE LINKAGE METHOD

TREE DIAGRAM

DISTANCES

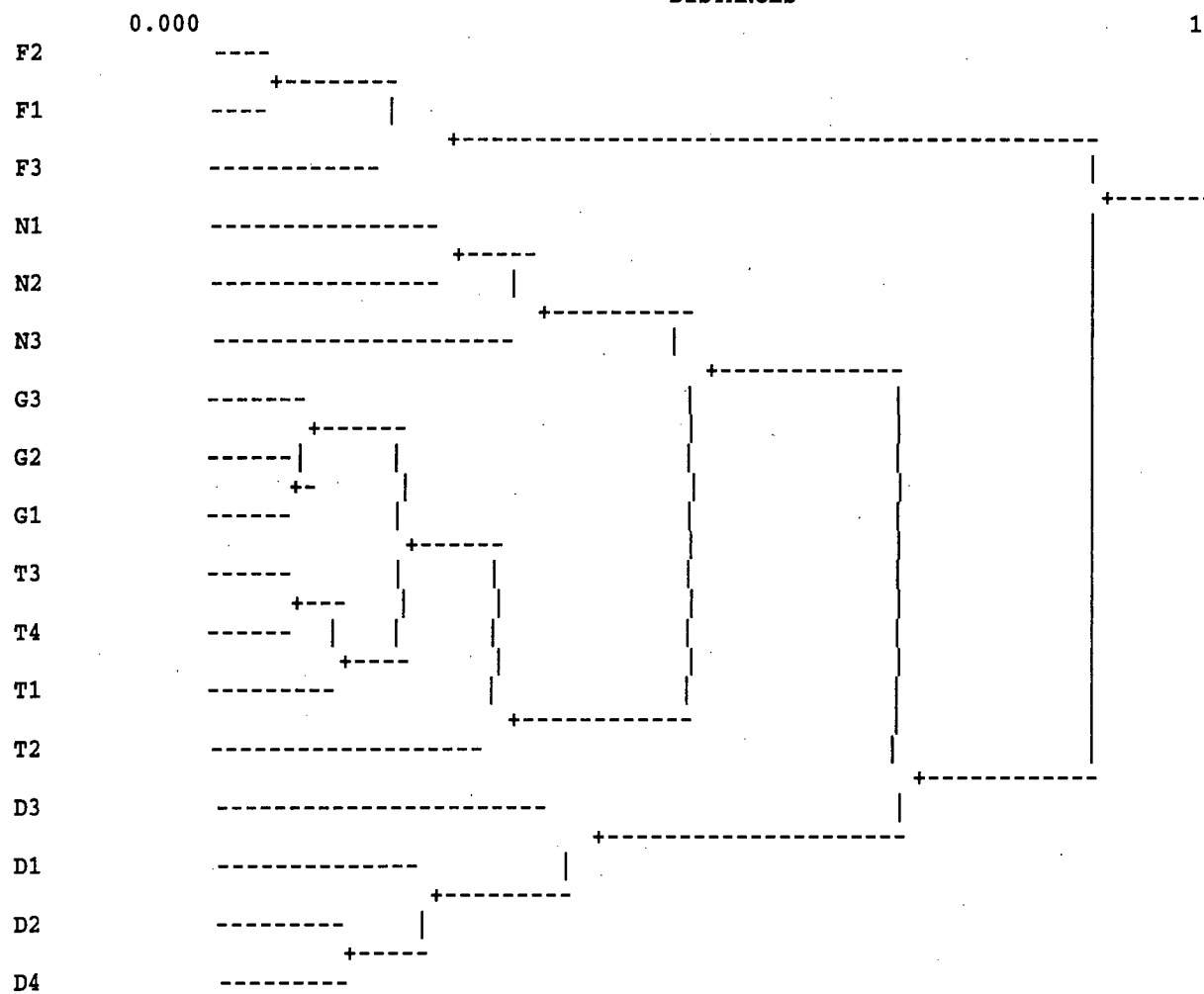
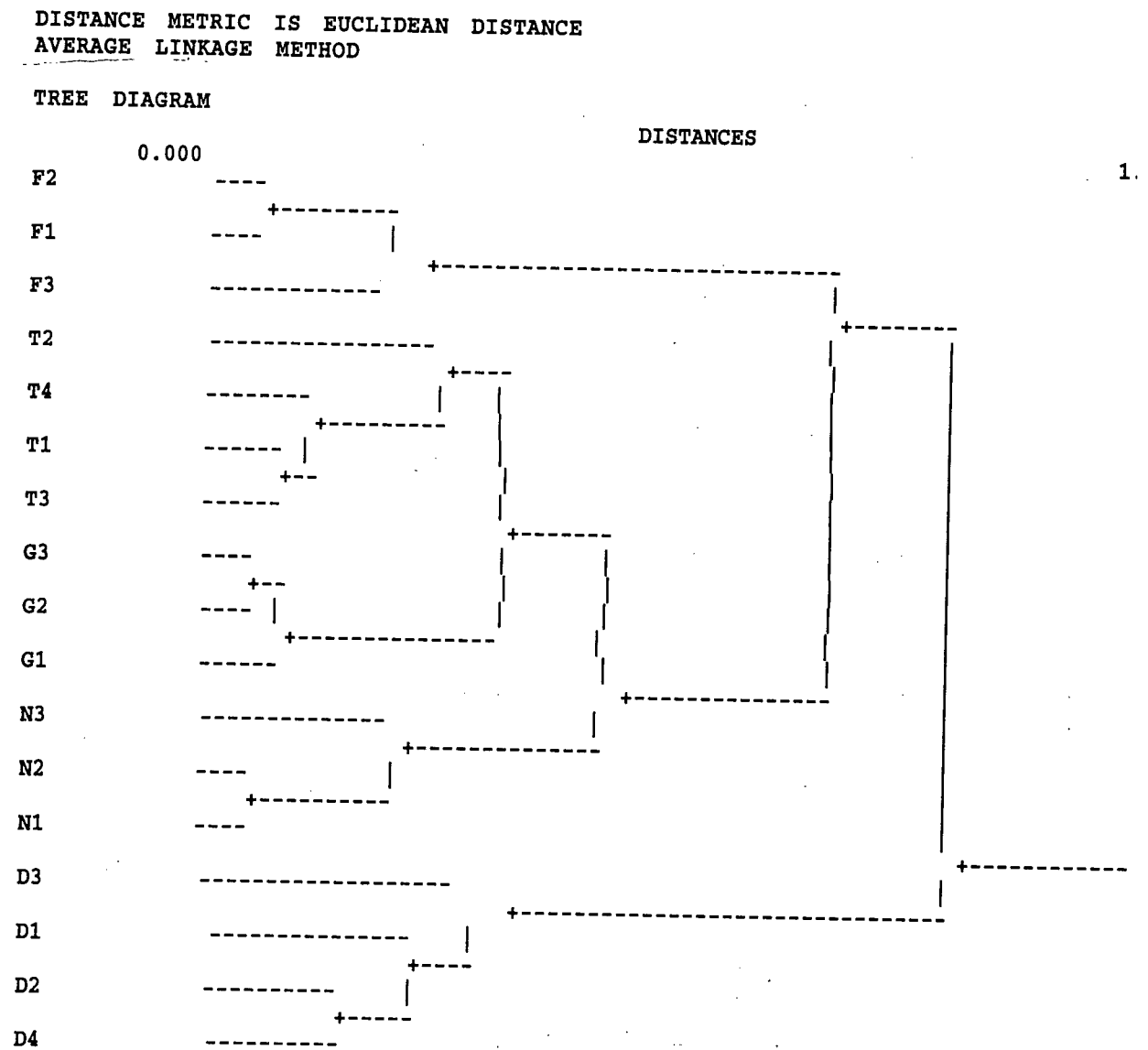


Figure 3.2.16. Cluster 4 - Transformed Measured and Categorical Variables



3.3 Transplant Studies

Of 120 *A. glabrum* seeds sown (1993 collection), 10% germinated (Table 3.3.1.), representing 3 var. *torreyi* populations and a single var. *glabrum* population. Following the appearance of cotyledons, all seedlings produced early leaves. These leaves were smaller, but of the same general shape as those observed on trees from which seed was collected (Figure 3.3.1.). A single, unusually vigorous seedling of population T1 (Lake Tahoe, California) also produced ternate (late) leaves on extension growth (Figure 3.3.1.d.), despite the fact that its siblings and the var. *glabrum* seedlings — under seemingly identical conditions — did not produce extension growth. Under the environmental conditions experienced by these seedlings at UBC (i.e., outside, without protection and with sub-optimal fertility and irrigation), extension growth and the development of late leaves was not expected. All other unprotected seedlings produced only early leaves.

Of 40 var. *neomexicanum* seed sown (Kelaidis, 1992 collection), 43% germinated. These seedlings grew rapidly under poly-tunnel conditions, producing 1 or 2 pairs of tiny, lobed leaves which were followed immediately by large, deeply-divided or ternate late leaves (Figure 3.3.1.b.). The majority of these seedlings grew more than 60 cm in each of their 1st and 2nd years. Under poly-tunnel conditions, growth appears to be nearly unrestricted, until shorter day length and cool temperatures induce dormancy.

All surviving scions grafted on *Acer davidii* performed poorly and produced little extension growth and few late leaves, except a single scion from population G3 (Bill Williams Mountain, Arizona), which produced ternate late leaves. Surviving scions on

Table 3.3.1. Collections and Transplant Results

Coll'n	Seed / Seedlings			Grafts					
	Sown	Germin- ated	w/ Late Leaves	Prepared		Surviving		Scions w/ Late Leaves	
				<i>rubrum</i>	<i>davidii</i>	<i>rubrum</i>	<i>davidii</i>	<i>rubrum</i>	<i>davidii</i>
D1	10	0		4	7	0	1	0	0
D2				3	8	0	0	0	0
G1	10	5	0						
G2				8	6	2	1	2 (1)	0
G3				6	4	0	1	0	(1)
N1	10	0		7	6	0	0	0	0
N2	10	0		8	3	0	1	0	0
N3	30	0		4	7	2	0	(2)	0
Nk†	40	17	(17)						
T1	20	2	(1)	14	12	0	5	0	0
T2	10	4	0	13	12	6	3	6 (1)	0
T3	10	1	0	8	8	1	4	(1)	0
T4	10	0		0	2	0	0	0	0

* numbers in parentheses are seedlings or scions producing 3-parted late leaves.

† Kelaidis collection (var. *neomexicanum* seed from Las Vegas, New Mexico)

Figure 3.3.1. Seedlings



a.) var. *glabrum*



b.) var. *torreyi*

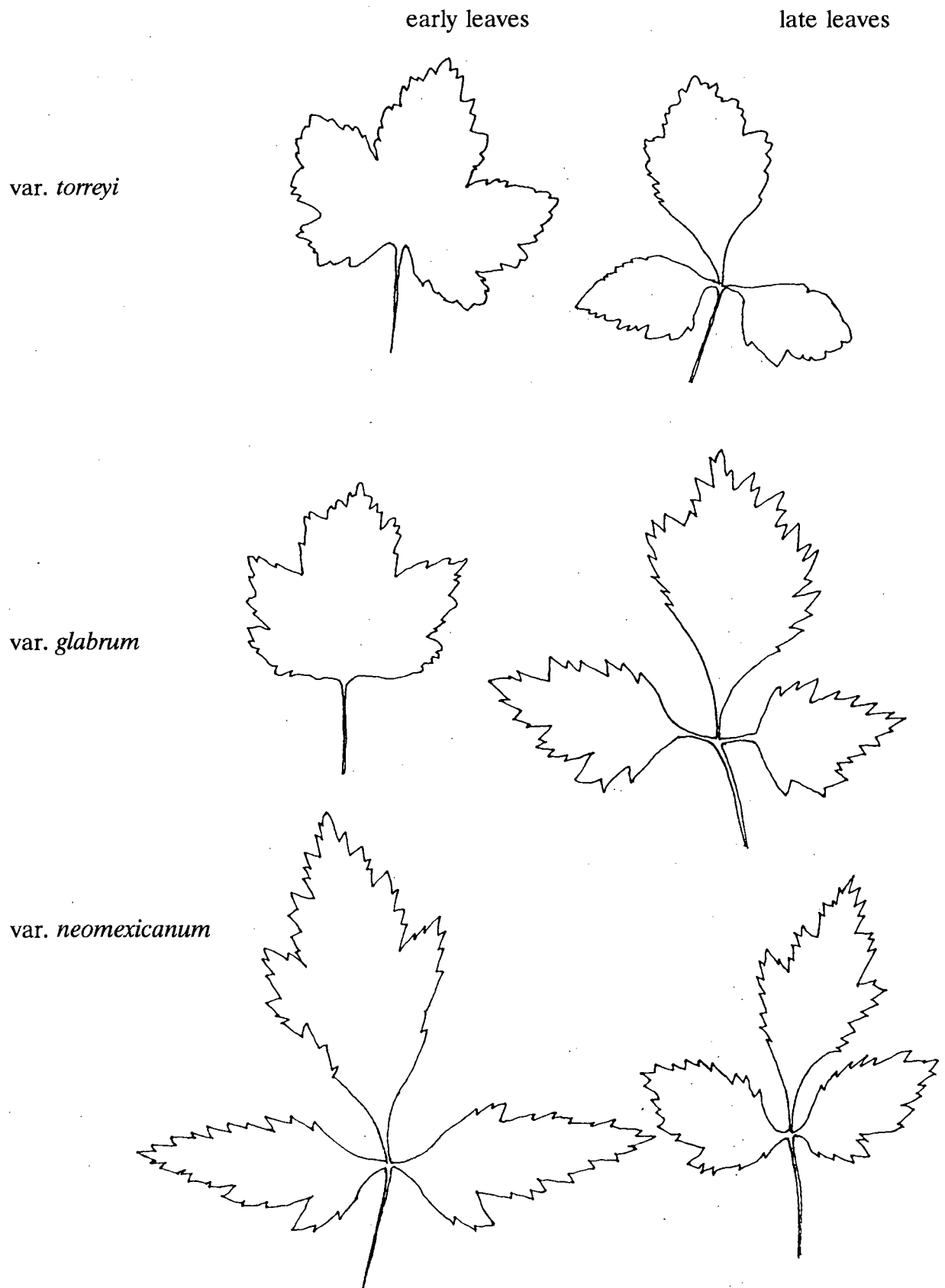


c.) var. *torreyi*



d.) var. *neomexicanum*

A. rubrum rootstock produced late as well as early leaves. Most late leaves produced were ternate. Only var. *douglasii* did not produce completely dissected leaves; those produced were more deeply lobed than the early leaves, but also appeared somewhat stunted. This may have been due to poor physical union of the scion and rootstock cambia. In nature, late leaves are seldom seen on var. *torreyi*, yet leaves produced by more than half of these scions were ternate and similar to those produced by varieties *glabrum* and *neomexicanum* (Figure 3.3.2.). Results of grafting trials are listed in Table 3.3.1.

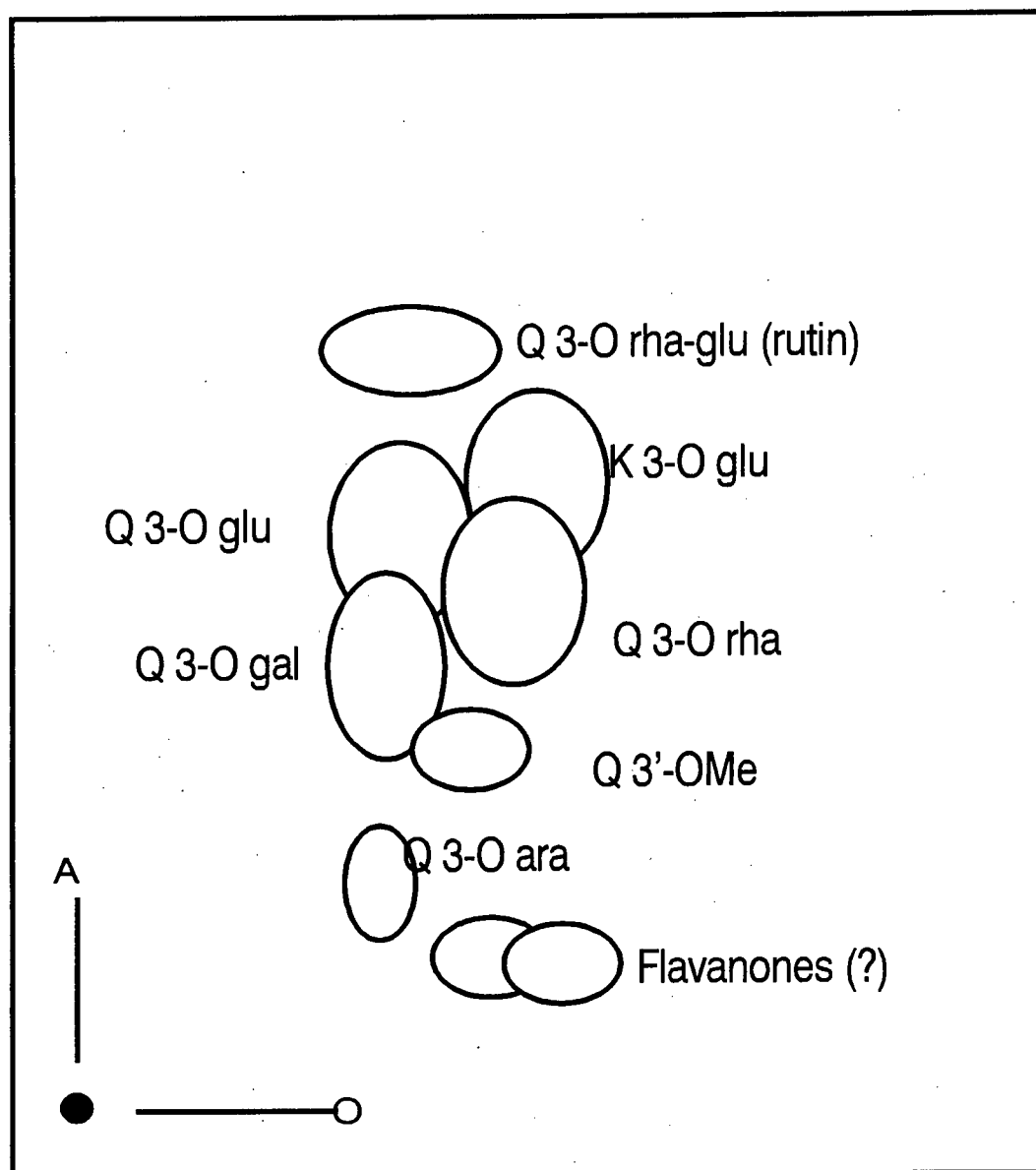


3.4. Flavonoid Analysis

Sampling of individuals both within and among populations showed that flavonoid profiles were constant throughout the species, supporting the findings of Delendick (1981) that each maple species produces a characteristic flavonoid profile. Analysis of leaves within individuals — i.e., extension versus non-extension leaves — also showed no variation.

The flavonoid profile (Figure 3.4.1.) was shown to consist of 2 unidentified flavanones, 2 kaempferol 3-O-monoglycosides, 2 quercetin 3-O-monoglycosides, rutin and isorhamnetin. Delendick (1981) reported flavonols, ellagic acid, pyrogallol and proanthocyanins in *A. glabrum*. Flavonoids not seen in the present study and reported by Delendick (1981) include fisetin, myricetin and apigenin glycosides. Previously unreported flavonoids identified in this study include flavanones and isorhamnetin. Flavonoids support the conclusion that all infraspecific taxa belong in a single species but are not useful in distinguishing those taxa. Flavonoids found in *A. glabrum* are listed in Table 3.4.1.

The observation of foliar flavanones in *A. glabrum* strengthens the admittedly strong relationship with sections *Arguta* Rehder and *Cissifolia* Koidzumi, and perhaps also the more tenuous connections with section *Indivisa* Pax. *Acer glabrum*, *A. cissifolium* and the species of section *Arguta* share many anatomical, reproductive (Ogata, 1967; Jong, 1994) and chemical traits (Delendick, 1981). *Acer carpinifolium*, the sole member of section *Indivisa*, has long been considered enigmatic, though Delendick (1981) considers the shared presence of apigenin and flavanones to link that section with *Arguta*. The

Figure 3.4.1. *Acer glabrum* Flavonoid Profile

Q = quercetin

K = kaempferol

rha -glu= rhamno- glucoside

rha = rhamnoside

glu = glucoside

ara = arabinoside

OMe = methoxyl (OCH_3)

presence of isorhamnetin in *A. glabrum* — previously reported in only the distantly related *A. macrophyllum* and *A. negundo* — probably represents an example of chemical convergence, since this flavonol has not been reported otherwise in the family.

Flavonoids common to section *Glabra* and related sections are listed in Table 3.4.2.

Table 3.4.1. Flavonoids from *A. glabrum*

Flavonoids	Present Study	Delendick (1981)
Flavanones	+	-
Fisetin	-	+
Kaempferol 3-O-arabinoside	-	+
Kaempferol 3-O-galactoside	+	+
Kaempferol 3-O-glucoside	+	-
Kaempferol 3-O-rutinoside	-	+
Quercetin 3-O-arabinoside	+	-
Quercetin 3-O-glucoside	+	+
Quercetin 3-O-rhamnoside	+	+
Myricetin 3-O-glucoside	-	+
Quercetin 3-O-rutinoside	+	+
Quercetin 3-O-xylosylgalactoside	-	+
Apigenin 7-O-diglycoside	-	+
Isorhamnetin	+	-

Table 3.4.2. Flavonoids from *Acer* Section *Glabra* and Related Sections (Modified after Delendick, 1981)

	Flavonoids*								
	Ap-C	Ap	Lut	K	F	Q	M	Iso	Flav
Sect. <i>Glabra</i>		+		+	+	+	+	+	+
Sect. <i>Arguta</i>		+	+	+	+	+			+
Sect. <i>Cissifolia</i>		+	+	+	+	+			+
Sect. <i>Indivisa</i>	+	+				+			+

* Ap-C = apigenin-C-glycosides; Ap = apigenin; Lut = luteolin; K = kaempferol; F = fisetin; Q = quercetin; Myr = myricetin; Iso = isorhamnetin; Flav = flavanones.

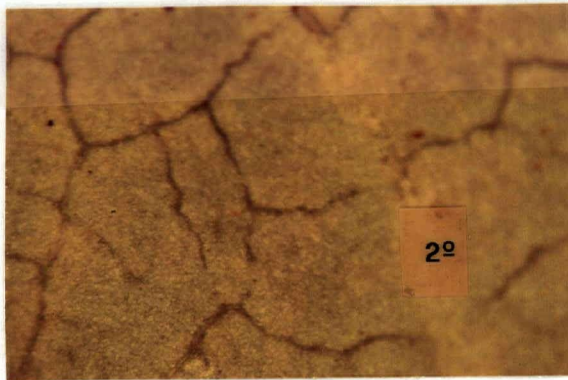
4.1. Field and Herbarium Studies

Trends in Morphology

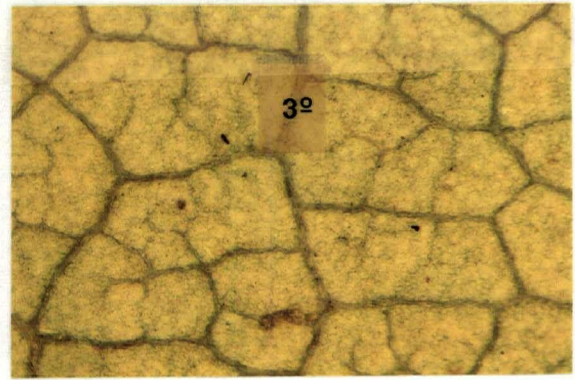
Variation in morphology (Table 3.1.2.) was observed within and among all populations visited, and within and among populations represented by herbarium specimens from specific taxon localities. Throughout the range of the species, increasing leaf size is correlated with larger overall plant size. Plants in the northern part of the range appear larger in all dimensions; i.e., leaf surface area, twig diameter, internode length, samara size and overall tree size. In the central part of the range, plant parts are comparatively smaller, and in the far south, plants are intermediate. Vein architecture (Hickey, 1973) is developed to the greatest degree in large leaves; here, 4th order veins are orthogonal and the areoles appear well-developed. The vein architecture of smaller leaves is increasingly more irregular as leaf size decreases. When not obscured by thickened abaxial cell layers, the 3rd and 4th order veins appear reticulate and the areoles are poorly developed (Figure 4.1.1., and see Table 3.1.2. for characterization of taxa).

Increasing leaf and marginal tooth size is correlated with increasing moisture availability and increasing latitude. Increasing leaf sinus depth is correlated with decreasing latitude and increasing moisture availability. The increasing indistinctiveness of higher order veins (due to the thickening of abaxial spongy mesophyll) is correlated with high summer temperatures and decreasing moisture availability. In addition to the trend toward larger samaras northward, there is a trend southward, and particularly in areas of inconsistent moisture availability, toward increasing variation in samara size, shape and wing angle. No discernable trend was found with respect to the presence or

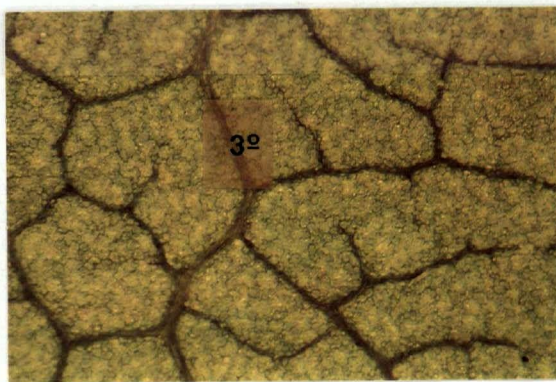
Figure 4.1.1. Vein Architecture (see Table 3.1.2. for explanation)



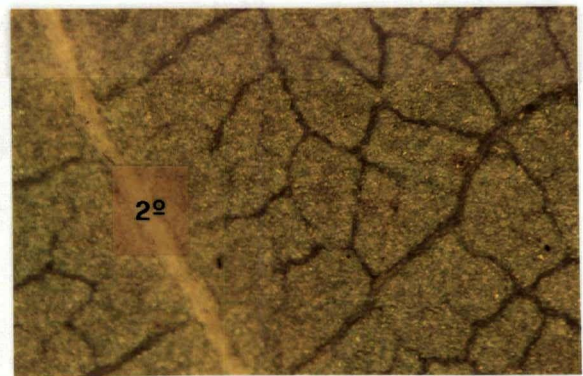
a) var. *diffusum*



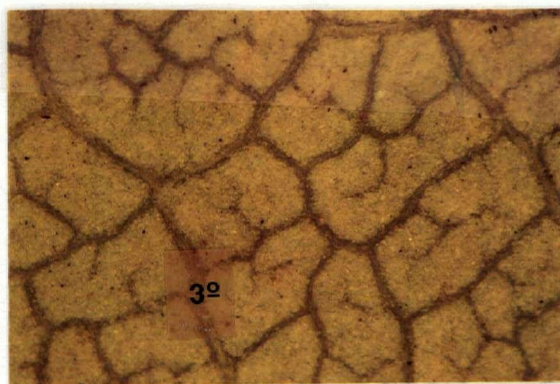
b) var. *neomexicanum*



c) var. *douglasii*



d) var. *torreyi*



e) var. *glabrum*

absence of samaras, either within or among populations. Within individuals, samaras were never found on branches exhibiting ternate leaves, except in southerly populations, where reproductive shoots exhibiting ternate leaves appears to be the norm.

Within-plant variation, characterized primarily by differences in leaf sinus depth, is most evident in the eastern part of the range. Increasing leaf sinus depth in these populations is correlated with extension growth and adventitious (particularly basal) shoots, 2 features most prevalent in areas of high temperatures and abundant summer moisture.

Studies to determine the effects of moisture and temperature on the preformation of leaves in *A. glabrum* would elucidate differences between many of the taxa. The presence of ternate leaves in the southern taxa is undoubtedly mediated by moisture availability, demonstrated by the increasing rarity of ternate leaves in varieties in habitats with increasing summer drought. The scarcity of 3-parted leaves in var. *douglasii*, however, may be a result of lower summer temperatures experienced in its habitats. It is likely that there is a critical set of temperatures below which, regardless of available moisture, extension growth and late leaves will not be produced. Similarly, as long as adequate moisture is accessible, there is probably a critical temperature beyond which terminal buds will not be set, and late leaves will continue to be initiated. Whether the geographical segregates are genetically differentially predisposed to temperature and moisture responses, can only be determined from long-term transplant studies.

Morphological Adaptations

Variation among geographical segregates of Rocky Mountain maple can presumably

be explained to a large degree by adaptations to specific environments (Table 3.1.2.). Low incident solar radiation and mesic conditions during the growing season in the north, and especially the northwest (due to forest cover, cloud cover and low sun angle), correlate with tall trees having broad leaves and shallow sinuses. Horn (1971) states that the most effective strategy for maximizing photosynthesis for broadleafed trees in shade is the regular spacing of large leaves where few overlap and where there are few gaps between them; i.e., a monolayer. This architecture is characteristic of var. *douglasii* throughout most of its range (Figure 4.1.2.a.). Horn (1971) states that more open situations (typical of the drier, warmer areas of western North America) are suited to multilayered trees, where randomly distributed smaller leaves do not overlap horizontally, and are far enough apart vertically so as not to shade each other. My observations of the southern varieties fit Horn's description of multilayered trees (Figure 4.1.2.b.).

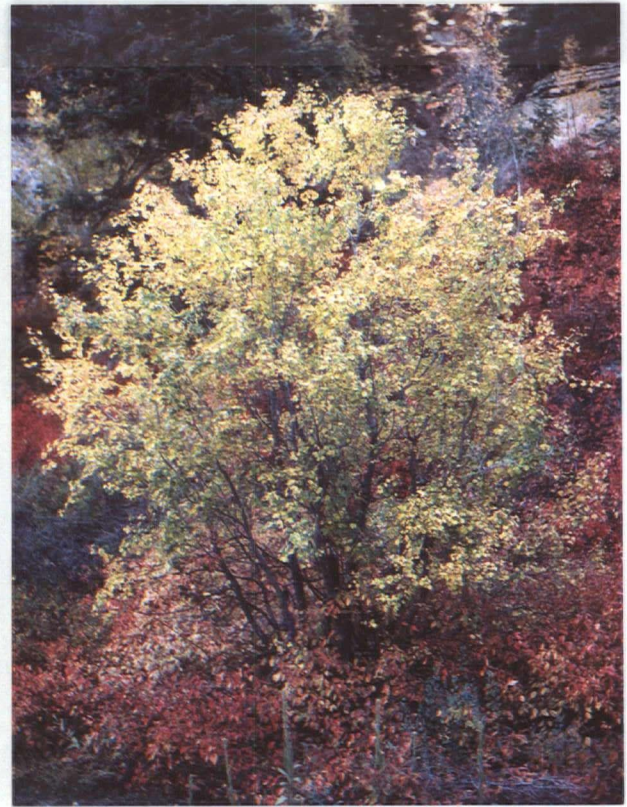
Reduced moisture availability appeared to result in less arborescent plants with smaller leaves. This situation was repeatedly observed in all southern populations visited during the study. I contend that lower overall transpirational flux is less able to support rapid growth and maintain large leaves, so internode length and individual leaf-blade surface area (photosynthetic surface) is decreased. Within populations, plants in closer proximity to draws, depressions or streams appear more robust in all dimensions than plants on apparently drier sites. However, even in riparian situations, stem thickness, leaf size or overall tree size never approach the proportions of var. *douglasii*, suggesting that the northern and southern varieties are genotypically distinct.

Large leaves in a hot, sunny climate are often a liability, since leaves are characteristically efficient at collecting light, and therefore, heat. A common adaptation among

Figure 4.1.2. Canopy Structure



a) Monolayer Canopy
var. douglasii



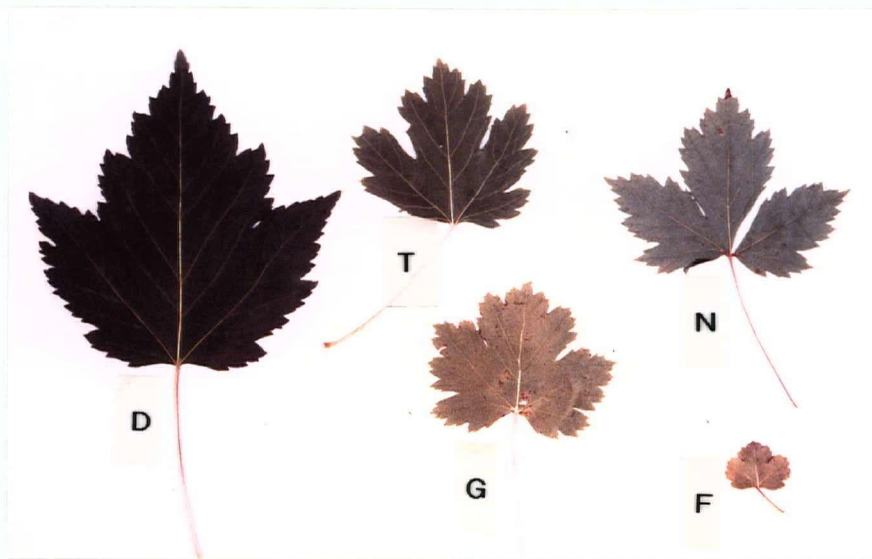
b) Multilayer Canopy
var. neomexicanum

dicots to prevent excessive heat build-up in leaves is the development of toothing, lobing or compounding. The exchange of heat and water vapour is faster around the edge of a leaf than in the centre of the lamina because the boundary layer is thinner at the edge (Monteith, 1973). In other words, the longer the edge surface, the better the radiator.

Maples growing in hot summer climates where moisture is consistently available throughout the growing season, often exhibit lobe apices and marginal teeth that are large and more or less acuminate, as well as deep sinuses. These modifications increase effective radiative surface while maintaining photosynthetic area. Variety *neomexicanum* (Figure 4.1.3.N.), and to a lesser degree, var. *glabrum* (Figure 4.1.3.G), exhibit these traits; this explains why, despite the high incident radiation in var. *neomexicanum* habitats (high elevation, low latitude), trees supplied with consistent, plentiful moisture are tall, with comparatively large leaves.

I believe that the compound (ternate) leaf is better adapted to high incident radiation than a simple palmatifid leaf of comparable surface area. Not only are such leaves inherently better radiators, but simple relaxation of the petiolules (the nastic mechanics may not be simple) aligns the leaflets vertically, significantly reducing light exposure to the blade surface. This alignment is analagous to the way that fragile newly emerging leaves are angled away from (i.e., parallel to) the sun's rays. The variety *neomexicanum* is characterized by ternate leaves that have a glaucous wax on their abaxial surface (Figure 4.1.3.N.). Involution or folding up of individual leaflet blades, a common response to water stress, exposes this reflective waxy surface and may contribute to a tissues burned-off during prolonged drought, acute lobe apices, the 2nd. Environmental constraints on the size and shape of lobes and marginal teeth necessitates the utilization

Figure 4.1.3. *A. glabrum* Leaves (Abaxial Surface)



D = var. *douglasii*; F = var. *diffusum*; G = var. *glabrum*; N = var. *neomexicanum*;
T = var. *torreyi*

reduction in heat loading.

In the western Great Basin and Sierra Nevada, where summer drought is a regular feature, populations of Rocky Mountain maple (i.e., varieties *diffusum* and *torreyi*) often show thickened leaves with blunted leaf apices and marginal teeth (Figure 4.1.3.F. and 4.1.3.T.). These are presumably adaptations to increased solar radiation and dry conditions. I suspect the absence of regular summer moisture is a strong selective force for the reduction of significant marginal toothing and lobe acuity — acute teeth being the 1st

of other leaf and stem modifications to reduce high potential heat loading and consequent water loss. Adaptations to xeric environments seen in these taxa include reduction in leaf surface area, canopy multilayering, thickening of abaxial cell layers and roughening of the abaxial surface.

Overall reduction in leaf size, with the tendency toward a reduction in lobing and ultimately — as seen in the xerophytic var. *diffusum* — to a near circular leaf outline (Figure 4.1.3.F.), decreases leaf boundary layer resistance (the smaller the leaf, the lower the resistance). This lower resistance facilitates the off-loading of heat by the increased movement of air. The multilayered canopy contributes to increased air circulation around leaves, further reducing boundary layer resistance (the higher the air velocity, the lower the resistance). On the abaxial surface, roughening increases boundary layer resistance around stomata (the rougher the surface, the higher the resistance), and the presence of a thickened spongy mesophyll layer facilitates the sinking of guard cells well below the abaxial epidermis. This increases the diffusion resistance of water vapour, thus effecting a reduction in transpirational water loss and therefore, overall water use.

Heterophylly

Like many woody plants, maples often exhibit variable leaf morphology over the life of the plant. Changes marking the transition between "juvenile" and "adult" stages in *Acer* are encountered in a few species (Jong, 1994). Critchfield (1971), however, reports that this type of heterophylly is ubiquitous in *Acer*, but my observations tend to support the more conservative view. This type of heterophylly is well expressed in some of the snake-bark maples (section *Macrantha* Pax). In many of these species, lobed leaves give

way to entire leaves upon reproductive maturation. In Rocky Mountain maple, a discrete juvenile stage (i.e., a morphology on non-reproductive shoots different from that on reproductive shoots) is not reported in the literature, nor was it observed in this study.

Similarly, changes which occur during the development of single annual adult shoots are common only in some species, and poorly expressed or unknown in others (Critchfield, 1971). This type of heterophylly has been studied in a number of maple taxa (Desmarais, 1952; Critchfield, 1971; Marks, 1975; Steingraeber, 1982), including *A. glabrum* (Steingraeber, 1984). Results from these studies and investigations of other temperate trees show that 2 developmentally distinctive routes are followed in the production of leaves on some shoots. Leaves which appear early in the season are initiated the previous year, and are termed *preformed* or *early* leaves. In many maples, 2 to 6 pairs of leaves are preformed and overwinter in buds as embryonic leaves or leaf primordia (Critchfield, 1971). In contrast, *neoformed* or *late* leaves mature in the same season in which they are initiated, and are the latest leaves to appear on the shoot. Late leaves are most common on leader shoots, especially those of saplings, and on shoots from adventitious buds, where extension growth is pronounced and vigorous. If shoots include both preformed and neoformed leaves, and these leaves are clearly dimorphic, they are referred to as *seasonally heterophyllous* (Steingraeber, 1982) (Figure 4.1.4.).

Studies in other temperate, seasonally heterophyllous trees, including *Betula* and especially *Populus*, correlate late leaves with an abbreviated embryonic phase and uninterrupted development from initiation (or an early stage of ontogeny) until they reach their final size (Critchfield, 1960). In contrast, early leaves develop in 2 distinct stages: the 1st phase is a prolonged, well-defined period during which the form of the

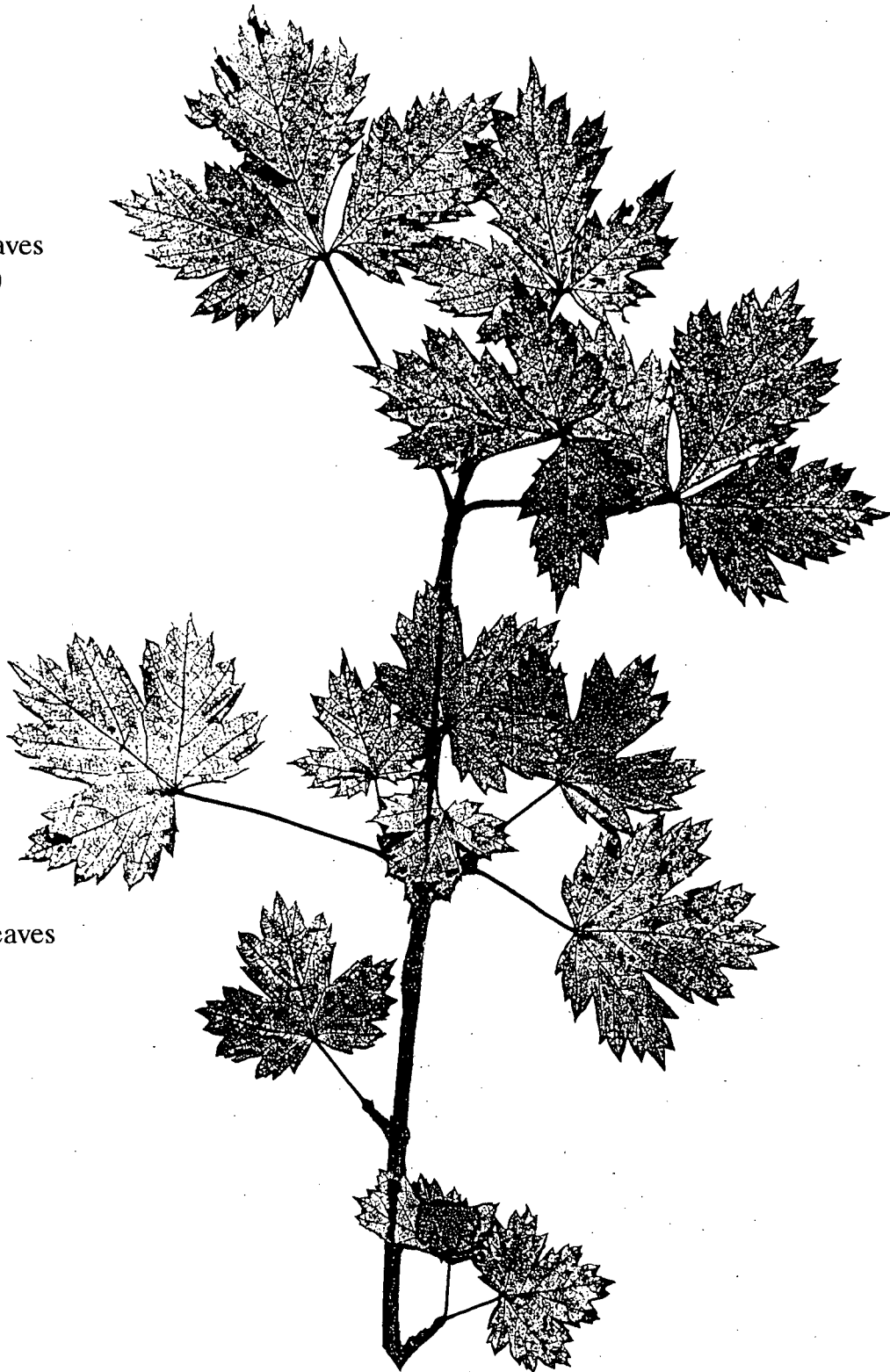
leaf is determined (Critchfield, 1971). Meijknecht (1965) reports that the shape of the 1st leaves in the winter buds of *A. palmatum* Thunb. is fully "blocked-out" by the time they are 0.5 mm long, and undergoes little change during later development. The embryonic phase of preformed leaves is separated from their expansion phase by a sharp boundary imposed by winter dormancy (Critchfield, 1971).

Seasonally heterophyllous leaves are common in Rocky Mountain maple, particularly the eastern and southern parts of the range. Here there has been much taxonomic confusion, especially where the number of dimorphic leaves is inconstant within or among trees and populations in a given year, or from year to year.

Early leaves in *A. glabrum* are normally three- to five-lobed; late leaves are usually more deeply divided or — especially in the southeastern taxa — ternate. Late leaves examined in this study show clearly that regions of the leaf most distant from primary and secondary veins, such as the leaf base and lobal subsinuses, have poorly developed lamina (Figure 4.1.5.). My observations suggest that the morphological differences are due to changes in the expression or activity of marginal and plate meristems of the developing leaves. It seems likely that preformation of leaves, i.e., protracted, 2 phase development, allows for an elaborate vasculature that can support higher plate meristem activity upon expansion the following spring. In contrast, rapidly initiated and expanded leaves cannot develop a vasculature extensive (or complex?) enough to bridge the broader regions between major veins. Presumably, in rapidly developing neoformed leaves, marginal meristematic activity outpaces submarginal meristematic growth (or outcompetes it for the allocation of water and solutes). That only meristematic regions nearest to terminating primary and secondary veins continue to expand in the ordinary

Late Leaves
(ternate)

Early Leaves
(lobed)

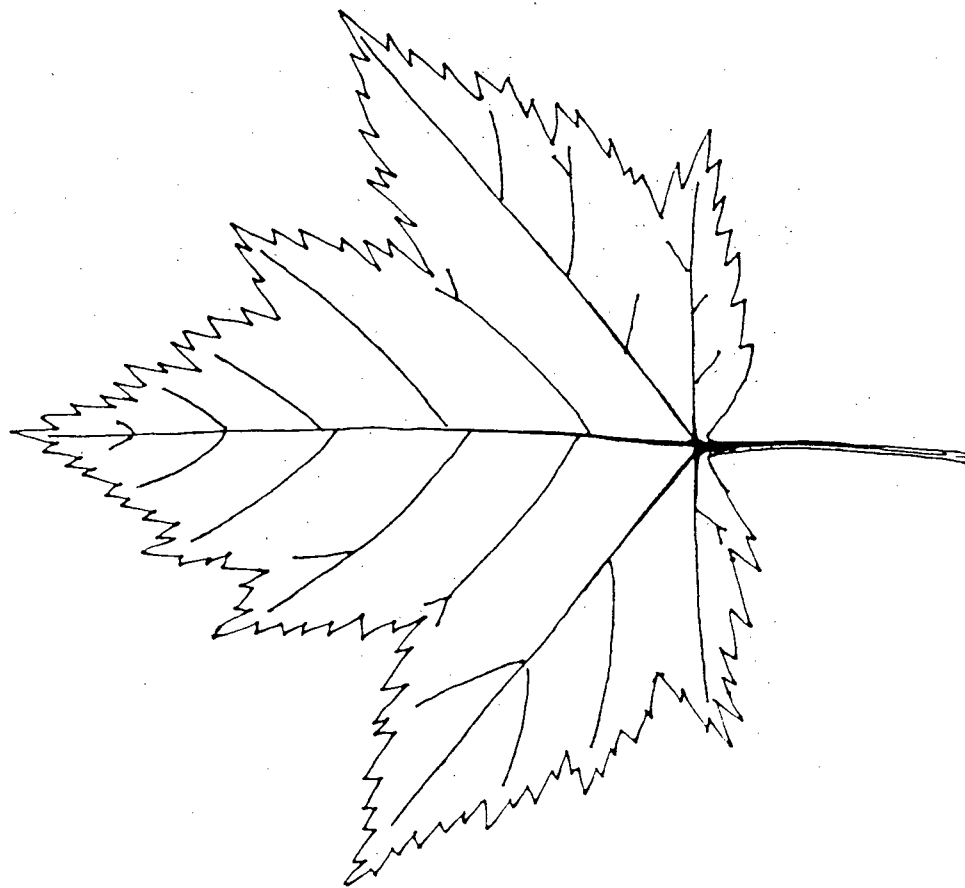


manner strongly suggests that submarginal meristematic activity is reduced or suppressed in rapidly growing neoformed leaves, relative to that in expanding preformed leaves.

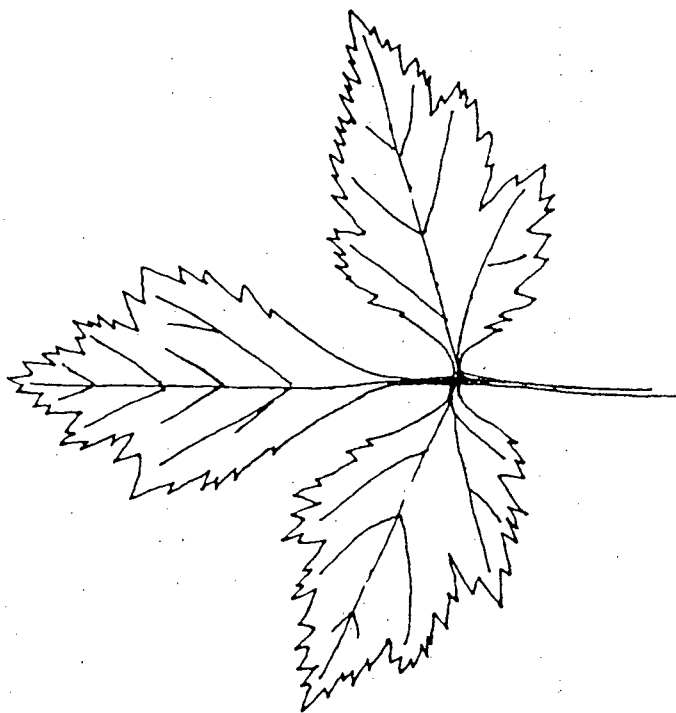
My observations indicate that summer moisture appears to mediate extension growth and the number of leaves produced on annual shoots. Thus, in relatively wet summers (or in moist areas), a significant proportion of the leaves will be neoformed and consequently deeply divided or ternate. In dry areas or in dry years, however, few late leaves will develop, and the majority of leaves will appear comparatively uniform and not deeply divided. A case in point is the ecad "tripartitum", which represents plants that display deeply divided to ternate leaves. In more or less the same geographical area, var. *glabrum* represents plants that exhibit mostly undivided leaves. Populations sampled in this area, as well as numerous herbarium specimens examined from this area, show both leaf-types and intermediates occurring. The degree of leaf division present on any single tree or branch is presumably correlated with the timing and availability of soil moisture.

The developmental line between preformed and neoformed leaves does not always appear to be distinctive. That is, the expression of typical early (lobed) leaves is most obvious in those 1st emerged, while ternate leaves, if they are produced, are conspicuous at some distance from the earliest leaves. Leaves produced midway between the 2 leaf-types are invariably larger than those first emerged and often somewhat intermediate in shape (it is unknown whether these leaves are entirely preformed or neoformed). With a single notable exception, it is the intermediate leaves that are considered characteristic for each recognized taxon. Variety *neomexicanum* (the exception) produces few if any intermediates; its characteristic leaves are almost always ternate and presumably neoformed. Although these leaves are usually produced following 1 or 2 pairs of small,

Figure 4.1.5. Leaf Lamina Comparison



var. *douglasii*



var. *neomexicanum*

lobed leaves, often only ternate or deeply divided leaves are produced.

Plants from cooler habitats generally produce more leaves per shoot that are not ternate. In this case, presumably, more leaves are preformed, or if neoformed, then at least their development is slow enough to allow significant subsinal blade growth. In contrast, trees from warmer regions have a propensity for producing ternate or deeply divided leaves. This suggests that few leaves are preformed (Steingraeber, 1984), and that neoformed leaves develop rapidly. Variety *neomexicanum* grows in mesic, often riparian sites, where growing conditions throughout the spring and summer appear optimal. I contend that because var. *neomexicanum* experiences a protracted growing season where terminal buds are set comparatively late in the season (very near to onset of winter dormancy), any preformation of leaves is probably abbreviated.

Taxa native to areas with a Mediterranean climate (characterized by warm or hot, dry summers and mild, relatively moist winters) rarely exhibit dimorphic leaves, except on rapid seedling growth, or on vigorous epicormic shoots. In these areas, a shorter growing season, either the result of seasonal drought or late spring/early autumn cold, could presumably effectively limit the ability of trees to produce late leaves on normal shoots. The southern Cascade/Sierran variant of Rocky Mountain maple, var. *torreyi*, does not appear to inhabit riparian sites, where optimal moisture conditions might confer a more frequent seasonal heterophyllous state. Competition from other plants, especially other, more shade-tolerant trees and shrubs, probably excludes *A. glabrum* from these habitats.

Variety *douglasii* inhabits a range of sites, from riparian to sub-xeric, yet even in moist sites, rarely produces ternate leaves. Here, cool temperatures and a comparatively short growing season probably restrict their development. Further, these plants may

preform more leaves than other *A. glabrum* segregates, and be capable of producing considerable extension growth without initiating neoformed leaves.

4.2. Morphometric Analysis

Principal Components Analysis

Principal Components Analysis (PCA) is a multivariate statistical technique for assessing variation. PCA creates uncorrelated indices, or *eigenvectors*, from combinations of existing variables in a multivariate data matrix. The lack of correlation is a useful property, in that it means that the eigenvectors are measuring different "dimensions" in the data (Manly, 1986). The 1st eigenvector describes the greatest amount of the inherent variation, the 2nd, the 2nd greatest, and so on.

The data set used in this study is a good candidate for PCA because most of the original variables are highly correlated. With such a data set, a small number of eigenvectors can adequately represent the variation expressed in a large number of original variables. However, the fact that the original variables are highly correlated underlines that most of them are measuring the same thing — in this case, mostly size. Nevertheless, PCA can graphically portray a substantial amount of variation in many fewer dimensions than the original multivariate data set, and may detect meaningful underlying dimensions. PCA is often used when bivariate techniques do not adequately portray complex shapes.

PCA was unable to resolve varieties *glabrum* and *torreyi*, given the factor score coordinates ascribed to each. This suggests there is little to discern them. Close examination of the shape and orientation of ellipses in Figure 3.2.12., however, reveals that the leaves of var. *glabrum* vary more with respect to factor 2 than factor 1, and that those of var. *torreyi* vary similarly with both factors. In other words, var. *glabrum* varies more in

shape than size, while var. *torreyi* varies in both shape and size. Compared with the resolution of the other infraspecific taxa, these differences are hardly profound (there is a greater degree of difference in orientation, shape and position between the 4 var. *douglasii* populations, for example).

On the other hand, it does not seem surprising that taxa exhibiting similarly sized leaves should fall together in an analysis based primarily on leaf size. That the 2 taxa are physically separated (and presumably have been for considerable time) and that there are qualitative differences in the leaves — such as in marginal tooth shape and leaf anatomy — affords little doubt that the 2 are biologically distinct. Ultimately, PCA fails to illuminate the dichotomy because the variables that would resolve the 2 taxa were either not included in the analysis, or are overshadowed by the large number of highly positively correlated variables. Unfortunately, the kinds of variables that best describe the differences between varieties *glabrum* and *torreyi* (i.e., mostly qualitative ones) are not suited to PCA.

Where PCA seems to be the most useful is in leaf-type comparisons (i.e., extension versus non-extension leaves) within taxa. Confidence ellipses (Figure 3.2.10.) show that all taxa have larger extension leaves than non-extension leaves, suggesting that preformation constrains ultimate leaf size. That extension leaves in var. *neomexicanum* are less variable than non-extension leaves (Figure 3.2.10.d.) suggests that either environmental conditions are less variable in its habitats once it begins to produce extension leaves, or that there are genetic constraints on the size and shape of these leaves. The more marked differences in position and orientation of leaf-type ellipses for both varieties *glabrum* and *neomexicanum* show that extension and non-extension leaves are more

distinct in these taxa. Indeed, the likelihood of extension leaves being ternate is far greater in these than any of the other taxa.

Cluster Analysis

Cluster analyses performed here demonstrate the problems inherent in data that has a bias toward a single character. The majority of variables used in initial clusters (Figures 3.2.13. and 3.2.14.) were size-related, with relatively high numerical values. The employment of these variables in clustering effectively reduced the influence of those variables for which numerical values were comparatively small. Only when the size component was discounted by log-transformations of all variables did clustering begin to reflect the geography of the infraspecific taxa (Figure 3.2.15.), and then only with the addition of qualitative characters did it reflect it accurately (Figure 3.2.16.). It must be kept in mind, however, that cluster analyses were based on population means. Mean values therefore represent a considerable loss of information compared to actual leaf measurements for individual trees. It is clear from field and herbarium studies and PCA scatter plots that there is profound variation within many populations, and it is doubtful that cluster analysis would appear as robust if mean leaf values from individual trees were used. (Analysis using mean leaf values from individual trees were attempted, however the problem was too comprehensive for the computer program.)

4.3. Transplant Studies

Seedling germination results were disappointing, falling short of reports in the literature (Schopmeyer, 1974), despite attempts to optimize conditions. Initial storage before stratification may have had an effect on enhancing dormancy of the viable seeds. Folkerts (1994, pers. comm.) reports that germination of Douglas maple (*A. glabrum* var. *douglasii*) is unpredictable from year to year, with sometimes less than 50 percent germinating in the 1st year, and a majority of the remaining seed germinating only after a 2nd winter. Alternatively, many of the fruits may have been parthenocarpic and hence, the seeds inviable. *Acer glabrum* fruits have a flattened, wrinkled nutlet which does not appear to differ in shape with respect to the presence or absence of a viable embryo.

Early leaves exhibited by both seedlings and grafted plants resembled the leaves of shoots from which they were derived, suggesting that the distinctive morphologies of these individual taxa are genetically fixed and not entirely subject to environmental manipulation. It may be that preformed leaves on scions were influenced (canalized) by the environmental conditions of the habitats from which they were collected. Seedlings also exhibited leaf-shapes typical for their taxa, however, and canalization of seeds does not seem likely.

In contrast, late leaves tend toward a ternate morphology. Although not seen in these transplant experiments, ternate leaves occur periodically in var. *douglasii*. At Reid, Collins Nursery, Aldergrove, B.C., occasional seedlings of var. *douglasii* are exceptionally vigorous and produce deeply divided or ternate leaves (Figure 4.3.1.). There, seedlings

Figure 4.3.1. var. *douglasii* Seedling with Ternate Leaves



are unprotected, but fertility and moisture are manipulated to near optimal levels. The appearance of ternate leaves on plants of taxa not commonly associated with this morphology (namely, varieties *douglasii* and *torreyi*) suggests that regardless of provenance, all infraspecific taxa have the inherent capacity to produce heteromorphic leaves, but that habitat constraints usually limit their manifestation.

There do not appear to be any previously documented *A. glabrum* transplant studies in the scientific literature to corroborate the findings of this transplant study. Nevertheless, there are a few cited examples of mature trees in common garden situations that have retained infraspecific differences. For example, Delendick (1981) lists *A. glabrum* var. *douglasii* and var. *glabrum* "trifoliate phase" specimens from the University of

Washington Arboretum. Unfortunately, I was unable to locate and verify the identities of either of these plants in a recent visit to that institution. Photographs of plants reputed to be varieties *douglasii* and *glabrum*, in Gelderen et al. (1994, plates 43 and 44) from the Esveld Arboretum, show distinct differences in leaf morphology after presumably many years under the same conditions.

The question of the genotypic validity of var. *diffusum* also remains unanswered, since neither seed nor scion material was available for this study. As with the majority of *A. glabrum* taxa, there is a paucity of living material in botanical gardens and arboreta. The var. *douglasii* is apparently the only regularly cultivated taxon, and it is only rarely grown. This information is based on my 1993 survey of 31 botanical and horticultural institutions in the United States and Canada, and 5 in the United Kingdom. It is presumed that var. *diffusum*, like the remaining geographically distinct segregates, is genotypically distinctive.

Graft Compatibility

The grafting of most maples is normally only possible using scions and rootstocks of closely related species; a physiological rejection of the scion usually results when the species used are not close relatives. Evidence from extensive grafting trials on often rare maple species led Vertrees (1991) to conclude that compatible species are normally those from the same series, or at least the same section. Since no *A. glabrum* seedlings were obtainable, and no information on other suitable rootstocks was available at the start of transplant studies, *Acer davidii* Franchet and *A. rubrum* were used. The choice of *A. davidii* was made based on its supposed phyletic closeness to *A. glabrum*. *Acer davidii* is a member of section *Macrantha*, reputed to be a primitive associate of section *Glabra*

(Delendick, 1981). *Acer rubrum* was chosen based on my own suspicions of a close relationship between the two. Preliminary observations on graft compatibility between *A. glabrum* and *A. rubrum* (section *Rubra* Pax) in this study suggest a closer relationship than is generally accepted, although Vertrees (1991) warns that a period of up to 3 years should be passed before a verdict is reached on graft success in maples.

Studies in the wood anatomy of maples by Ogata (1967) support a close relationship between the sections *Rubra* and *Glabra*, and speculations by Jong (1976) link those sections as "uncertainly or questionably related". In contrast, more recent treatments (Tanai, 1978; Delendick, 1981; Jong, 1994) place the 2 more distantly, on the basis of chemical, morphological, palynological and reproductive features. That scions on *A. davidii* performed poorly or not at all, merely gives credence to Vertrees' general rule that one should pair rootstock and scion from within sectional confines for graft-compatibility. It does underscore, nevertheless, the possible significance of an *A. glabrum* - *A. rubrum* compatibility.

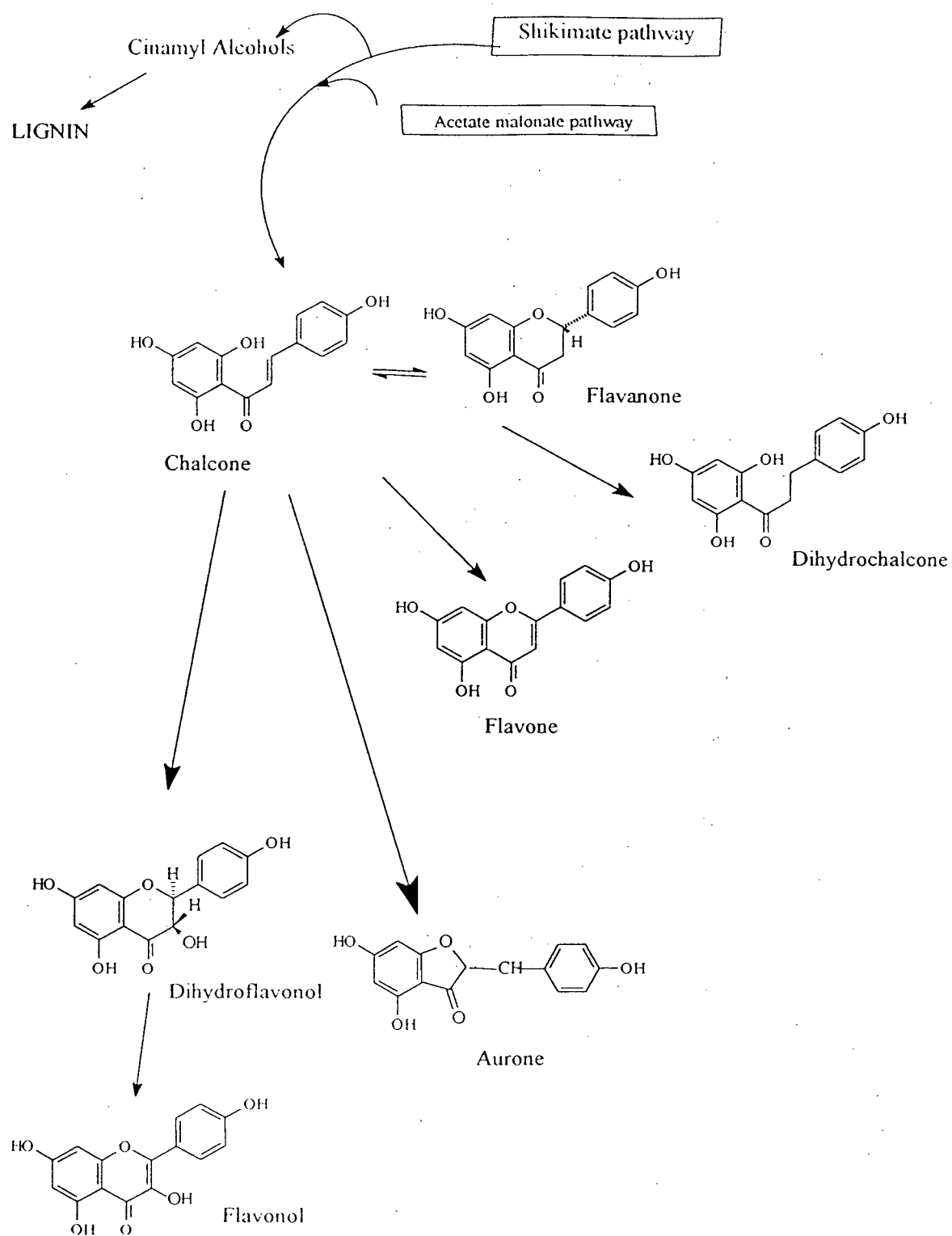
4.4. Flavonoid Analysis

Secondary plant products, i.e., those derived from primary metabolism, have proved useful in biosystematic research. By far, the most useful secondary metabolites are the phenol derivatives called *flavonoids* (Figure 4.4.1.). Many of these compounds are foliar pigments and/or insect feeding deterrents. Reasons for their utility are numerous, and include their ubiquity among higher plants, their wide range of discrete chemical structures, their stability, and ease of isolation and determination. Flavonoids are useful at various taxonomic levels in most plants, especially at lower taxonomic rank (e.g., genus, species and interspecific hybrids). Crawford (1978) posits that simple genetic differences likely control the classes of flavonoid compound present, and this allows for a high degree of biochemical variation at the lower taxonomic levels.

Flavonoids have been studied in maples (Delendick, 1981; Chang, 1990; Chang and Giannasi, 1991; and see Delendick [1981] for a summary of flavonoid reports to 1981). Delendick's (1981) *Systematic Review of the Aceraceae* is based primarily on flavonoid analysis of 188 maple species (including *A. glabrum*) and numerous cultivars. Among his findings relevant to this study are: that each maple species produces a stable and reproducible flavonoid profile; that isorhamnetin compounds are restricted to *A. negundo* and *A. macrophyllum*; that flavanones are absent from *A. glabrum*.

This study investigated 5 infraspecific taxa in *A. glabrum* — including plants known as subsp. *siskiyouense* and var. *greenei*, both of which are now referred to var. *torreyi*. In his systematic review of the Aceraceae, Delendick (1981) surveyed only 3 *A. glabrum* infraspecific taxa, omitting the varieties *diffusum* and *neomexicanum*, and including only a

Figure 4.4.1. Biosynthesis of Flavonoid Classes (after Markham 1981)



single specimen of var. *torreyi*. The flavonoid profile of Rocky Mountain maple observed in this study differs notably from that of Delendick with respect to the presence of flavanones and isorhamnetin, but does not affect the conclusion that all infraspecific taxa belong to a single species. The observation of foliar flavanones in *A. glabrum* strengthens the presumed relationships with sections *Arguta* and *Cissifolia*, and perhaps also the connections with section *Indivisa*. Links to these sections have also been made through morphology, anatomy, reproductive features and historical plant geography.

5.1. *Acer* Section *Glabra*

Acer L. Section *Glabra* Pax, Bot. Jahrb. 7: 217 (1886).

Lectotype: *A. glabrum* Torrey (Murray, 1970)

Deciduous trees and shrubs. Leaves chartaceous, undivided, 3-5-lobed, or barely ternate; margins serrate. Bud scales 2-4-paired. Inflorescences small, corymbose or racemose, terminal and axillary. Flowers 5-merous, stamens 8 (7-9); discs intra- to amphistaminal. Nutlets flat, glabrous, strongly veined. Includes only *Acer glabrum*. Western North America.

Taxonomic History

Ferdinand Pax produced the 1st modern systematic treatment of *Acer*. Pax (1885, 1886, 1893) recognized 4 major (taxonomically unranked) groups in *Acer*, based primarily upon the presence and position of a floral nectiferous disc. Sections within his groups (many of which still stand today) are based on leaf morphology, inflorescence type and fruit characteristics.

Interspecific Affinities

Many authors consider sections *Glabra* Pax and the East Asian *Arguta* close relatives (Pojarkova, 1933; Murray, 1970; Delendick, 1981), or "sister-taxa" (Ogata, 1976; Wolfe and Tanai, 1987). Jong (1976, 1994) submerges series *Arguta* Rehder in section *Glabra* following Momotani (1962). Delendick (1981), however, indicates that from an analysis of morphological, phytochemical, palynological and floral attributes, sections *Glabra*,

Macrantha Pax (the snake-bark maples), *Indivisa* Pax (the monotypic Japanese *A. carpinifolium* Siebold & Zuccarini) and *Arguta*, are approximately equally distantly related.

Morphologically, the leaves of *A. glabrum* var. *neomexicanum* and *A. cissifolium* Siebold & Zuccarini (Section *Cissifolia* Koidzumi) are strikingly similar (Figure 5.1.1.). Variation in *A. cissifolium* does not extend to simple, lobed leaves as it does in *A. glabrum*, except on early seedling leaves (Ogata, 1967). There is an admitted danger in drawing relationships (especially phylogenetic) based on leaf morphology, particularly in a genus replete with examples of convergence. Nevertheless, an argument can be made in support of a phylogenetic relationship between the 2 species, since there are established morphological, chemical, anatomical and reproductive links (Ogata, 1967; Jong, 1994; Delendick, 1981).

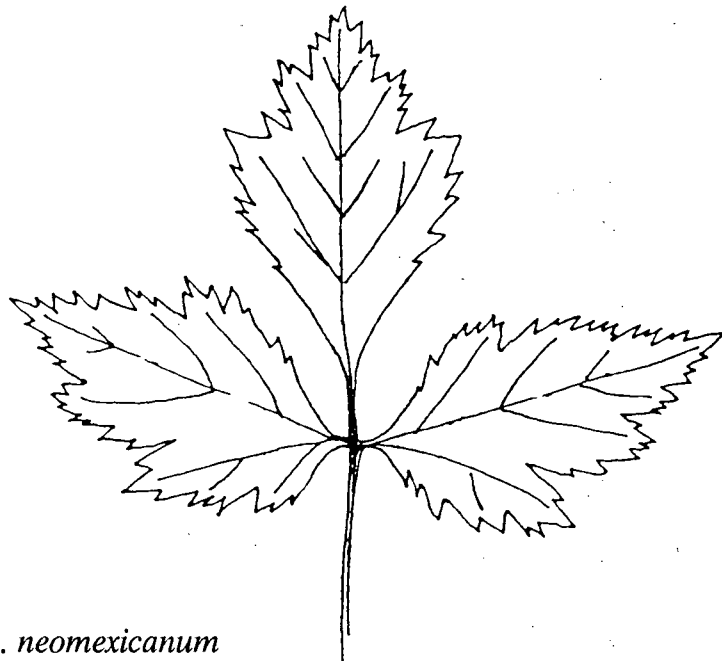
Phyletic changes in the timing of development (heterochrony) is assumed to be a source of much evolutionary diversification (Gould, 1977; Takhtajan, 1972, 1991). For example, changes in the ontogeny of leaves and shoots — i.e., elaboration or abbreviation of developmental stages — have presumably led to novel adaptations and, with sufficient reproductive isolation, new species in *Acer*.

In this respect, the late leaves of *A. glabrum* may represent a developmental elaboration of a strictly simple-leafed species, while the leaf characteristics of *A. cissifolium* represent a developmental truncation of the early (i.e., simple, lobed) leaf stage of *A. glabrum*. Simple-leafed ancestor candidates include the close relatives of *A. glabrum* in the eastern Asian section *Arguta* Rehder, or their progenitor, or *A. rubrum* (an eastern North American native), or its progenitor. Without adequate fossil

Figure 5.1.1. *Acer cissifolium* and *A. glabrum* var. *neomexicanum* Leaves



Acer cissifolium



A. glabrum var. *neomexicanum*

evidence, the ancestral and derived conditions in these species are difficult to ascertain.

According to Wolfe and Tanai (1987), all of the above-mentioned sections were present in the Eocene flora of western North America, so were presumably supplied the proximity, topographic heterogeneity and time scale required for adaptation and divergence. Following the cladistic analysis of extinct and extant sections of *Acer* by Ogata (1976), Wolfe and Tanai place all of the sections in the same clade (Figure 5.1.2.), although some authors differ (Delendick, 1981; Jong, 1994) on this analysis of sectional relationships.

Fossil History

The Aceraceae has been variously postulated as originating as part of the Arcto-Tertiary flora; in East Asia (Pax, 1926; Pojarkova, 1933); in Laurasia (Raven & Axelrod, 1974); in western China (Chien & Fang, 1934); in the Tethyan region (Croizat, 1952); and in western North America (Wolfe & Tanai, 1987). The most extensive review of palaeobotanical data for *Acer* since Pax (1885, 1886) and Walther (1972) (European maples only), supports the hypothesis of a western North American origin for *Acer* (Wolfe & Tanai, 1987). Those authors venture that not only did the family and genus originate in western North America, but that the major sectional diversification of the genus occurred here during the Eocene as well.

Sectional relationships

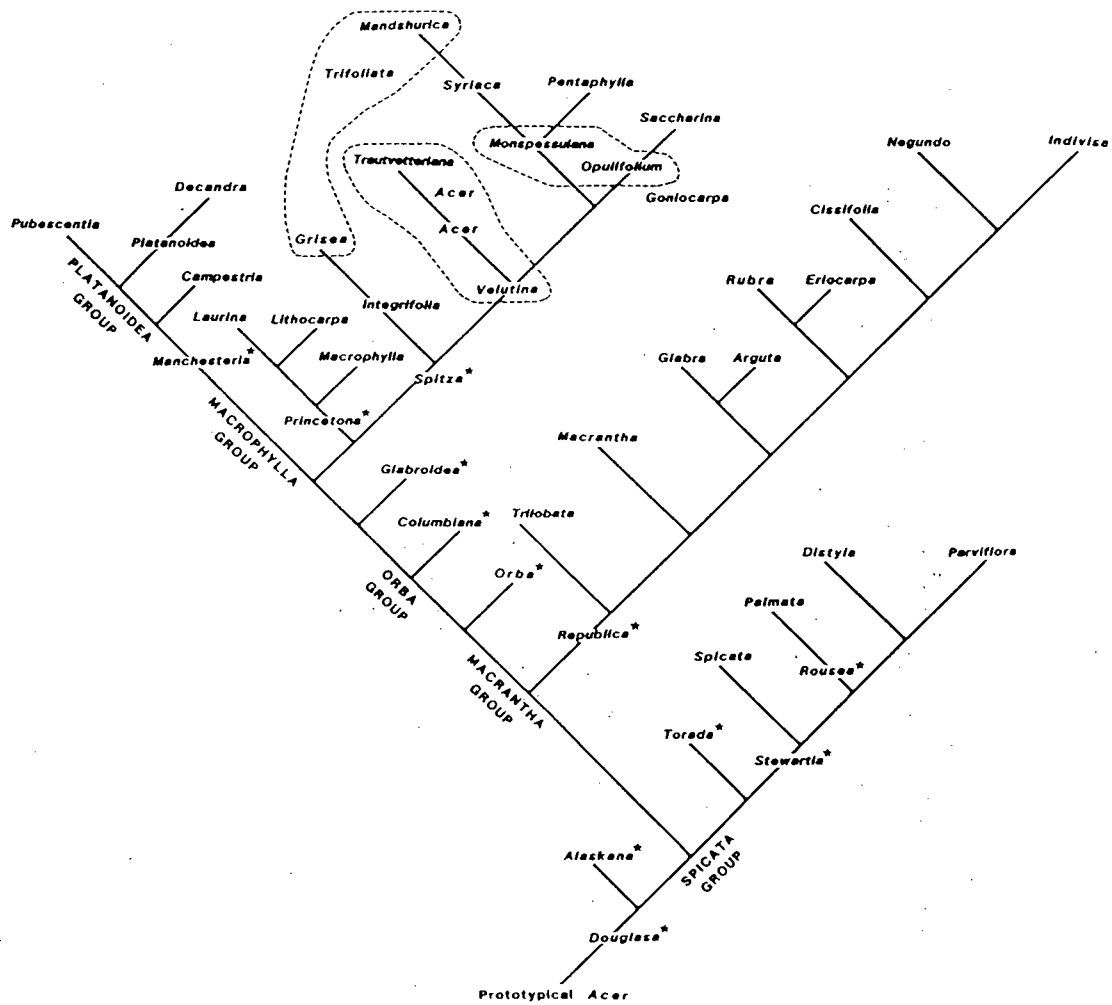
Section *Glabra* is represented in the fossil record by *A. (neomexicanum)* (Axelrod, 1988) and *A. traini* Wolfe & Tanai. Axelrod (1988) uses no fossil species names, but

rather, parenthetical taxa, which indicate their modern affinities. Axelrod (1988) cites *A. (neomexicanum)* as belonging to the Creede Flora. Curiously, the work upon which he presumably based his later comments — *The Late Oligocene Creede Flora, Colorado* (Axelrod, 1987) — lists only *A. riogrande*, an entity he associates with the undissected-leafed *A. columbianum* Chaney & Axelrod (1959). He suggests in the 1987 work that either of these 2 taxa are the likely progenitor of, or are conspecific with *A. glabrum*. The extant, dissected-leafed *A. neomexicanum* he connects with *A. coloradoense* MacGinitie (1941) from the Florissant beds. However, *A. columbianum* is listed in synonymy under *A. medianum* Knowlton (1902), in section *Columbiana* Wolfe & Tanai (1987) by Wolfe and Tanai (1987). Those authors refer *A. coloradoense* to *Rubus coloradoense* Wolfe & Tanai (1987), and ignore *A. riogrande*.

Occurrences of *A. trainii* are reported from the following assemblages: Chilcotin River, B.C. (Early Miocene); Purple Mountain, Nevada, Thurston Ranch, Nevada, Mascall/White Hills, Oregon (late Early to middle Early Miocene); Trout Creek, Oregon, Trapper Creek, Idaho (late Middle to early Late Miocene). *Acer trainii* is based entirely upon fruits which are typical of the "*Acer glabrum* type", i.e., prominent folds on the nutlet and the proximal and distal ends of the nutlet forming straight lines with respect to the margins of the wing (Wolfe and Tanai, 1987). Since no foliage has been associated with *A. trainii*, and the assumed environment and range of that entity appear to be similar to *A. glabrum*, this suggests that the fossil and extant species may be conspecific (Wolfe and Tanai, 1987).

The purported sister-group of the western American section *Glabra*, section *Arguta* (the extant species of which are entirely East Asian) is known in western North America

Figure 5.1.2. Cladogram of Extinct and Extant Acer Taxa (after Wolfe & Tanai, 1987)



from the fossil *A. ivanofense* Wolfe & Tanai. This taxon is represented by a single leaf from an early Late Eocene assemblage from the central part of peninsular Alaska (Beringia) (Wolfe and Tanai, 1987). It is supposed that the disjunction between *Arguta* and *Glabra* dates from the terminal Eocene climatic deterioration (Wolfe and Tanai, 1987). Unfortunately, there is an inconvenient lack of further evidence for this or any other palaeobotanical relationship with *A. glabrum*.

Palaeo-Distribution

Judging by the available fossil evidence, *Acer* was widespread in western North America prior to the Pliocene (Wolfe and Tanai, 1987), when vast areas experienced a humid microthermal climate (Wolfe, 1987; Axelrod, 1988). Gradual southward migration and extinction of maples occurred as a result of decreases in both summer temperatures and precipitation at higher latitudes during the Miocene (Wolfe, 1987). In the south, the annual temperature gradient increased and summer rainfall decreased, causing migrations of microthermal taxa to higher altitudes in the east and north, and coastward (Axelrod, 1988). The general increase in altitude at the lower latitudes — viz., the uplift of the Rockies, Sierra, Cascades and Coast Mountains in the Neogene — increased rain shadow effects in the Great Basin and east of the Rockies, and created a significant bottleneck for maples and other microthermal taxa. During the Pleistocene glaciation, this winter cooling-summer drying trend was accentuated, presumably resulting in all extant western North American *Acer* taxa being driven south of the glacial boundary in coastal or mountain refugia.

Intermontane regions south of the glacial boundary have limited Pleistocene fossil

floras that include maples. Axelrod (1988) describes the western North American Pleistocene flora south of the glacial boundary as similar to the extant flora for the same area, with the exception of southern California, where most of the Rocky Mountain Flora (including maples) had been eliminated because of the pronounced summer drying trend.

Early Holocene distribution of *A. glabrum* in western North America can be inferred from present distributions and ecological preferences. During interstadial and post-Pleistocene hypsithermals (stable, long term, high temperature [xerothermic] events), there was migration by microthermal taxa into humid to subhumid areas of increasing altitude and latitude, and overall range expansion in humid lowlands by warm microthermal taxa. The most recent hypsithermal, 5000 to 8000 years ago, was characterized by higher summer evaporation and temperatures, and lower summer rainfall than those of today.

Populations of *A. glabrum* var. *diffusum* in the desert and southwest mountains of southern California and the isolated mountain ranges of the Great Basin are clearly relicts of once larger populations, reduced either by hypsithermal or Pleistocene events. They represent the only surviving non-fluviatile maple in this area. The combination of convectional rainfall and winter snow accumulation on high mountain peaks appears to supply enough moisture for these plants to survive and reproduce, but not to expand their ranges. Presumably, *A. glabrum*, along with other microthermal taxa, have gradually reestablished their presence at lower latitudes and altitudes since the last hypsithermal, except in areas of significant rain shadow effect.

5.2. *Acer glabrum* Torrey

Acer glabrum Torrey, Ann. Lyc. Nat. Hist. NY 2: 172 (1828). Rocky Mountain maple.

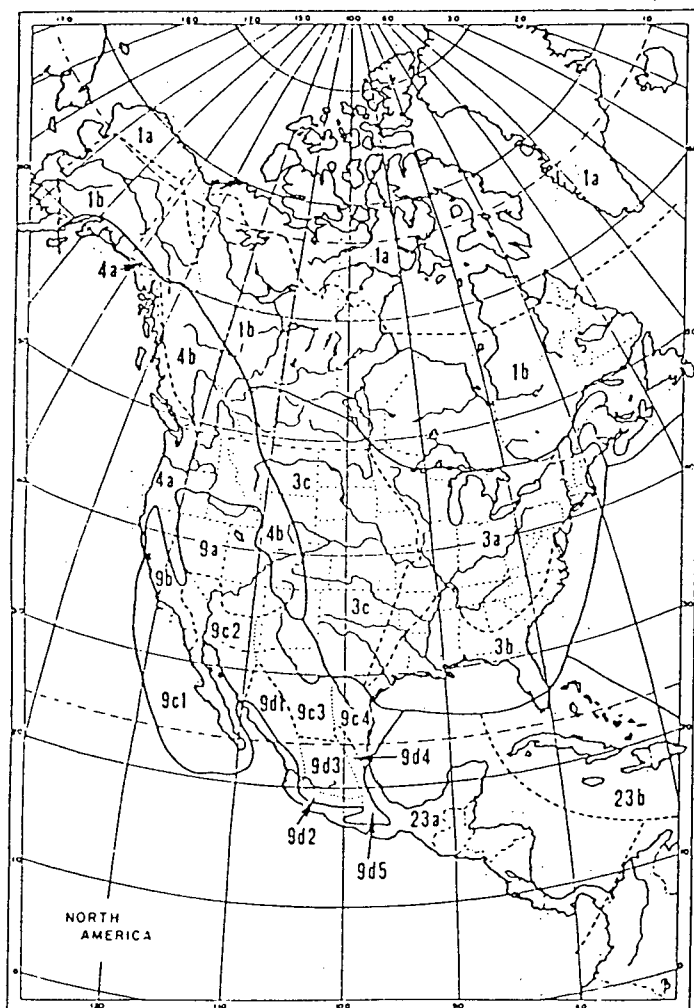
Holotype: Dr. James, in the Rocky Mountains about latitude 40 degrees (NY).

Rounded, glabrous shrub or tree, 2-10 m tall; twigs reddish-brown, greyish to whitish; petioles reddish, glabrous, 1-9.5 (-12) cm long; leaf blades broadly cordate, 3-5-lobed to 3-parted, truncate to subcordate at base, 1.2-13 (-16) cm long, 1.2-11 (-18) cm wide; leaf margin doubly and irregularly serrate, lobes or leaflets cuneate to rhomboid; bud scales tomentose on inner surface, outer pair of bud scales hard, shiny, deep scarlet, 0.5 cm long, middle rank rose-coloured, 1 cm long and inner pair yellowish, 2-3 cm long; flowers glabrous, monoecious to dioecious, 0.7-1 cm in diameter, borne in corymbs; length of peduncle plus pedicel 2-7 cm; stamens 8 (7-9), perigynous, 1/2 to 5/6 length of sepals in sterile flowers, much shorter in fertile flowers; sterile flowers staminate, linear petals as long as spatulate sepals; fertile flowers perfect, petals 1/4 to 1/2 as long as sepals; samara pairs 2-6 (8), glabrous, wings overlapping each other to widely divergent (130°), 1.5-4.5 (6) cm long; immature fruits reddish, changing to green and reddish with maturity. (Torrey, 1828.)

Distribution

The range of Rocky Mountain maple includes areas within both the Rocky Mountain and Madrean Floristic Regions of the Holarctic Kingdom (Takhtajan, 1986) (Figure 5.2.1.), an expanse that includes much of North America west of and including the Rocky

Figure 5.2.1. Floristic Regions of North America (after Takhtajan, 1986)



HOLARCTIC KINGDOM

FLORISTIC REGIONS AND PROVINCES OF NORTH AMERICA

LEGEND FOR MAP

1. Circumboreal Region.
 - 1a. Arctic Province.
 - 1b. Canadian Province.
3. North American Atlantic Region.
 - 3a. Appalachian Province.
 - 3b. Atlantic and Gulf Coastal Plain Province.
 - 3c. North American Prairies Province.
4. Rocky Mountain Region.
 - 4a. Vancouverian Province.
 - 4b. Rocky Mountain Province.
9. Madrean Region.
 - 9a. Great Basin Province.
 - 9b. Californian Province.
 - 9c. Sonoran Province.
 - 9c1. Baja Californian Subprovince.
 - 9c2. Sonoran Subprovince.
 - 9c3. Chihuahuan Subprovince.
 - 9c4. Tamaulipan Subprovince.
 - 9d. Mexican Highlands Province.
 - 9d1. Sierra Madre Occidental Subprovince.
 - 9d2. Trans-Mexican Volcanic Belt Subprovince.
 - 9d3. Mexican Altiplano Subprovince.
 - 9d4. Sierra Madre Oriental Subprovince.
 - 9d5. Sierra Madre del Sur Subprovince.
23. Caribbean Region.
 - 23a. Central American Province.
 - 23b. West Indian Province.

Mountains.

Acer glabrum ranges as far north as the Lynn Canal (Piper and Beattie, 1915) in southeastern Alaska, east to the Rockies and southwestern Alberta, following the cordillera south to the central and southern Rocky Mountains, spilling over into northwestern Nebraska (Little, 1976; McGregor et al., 1986) and terminating north of the Mexican border in New Mexico (Rydberg, 1922; Little, 1976; Martin and Hutchins, 1980). A disjunct population is commonly reported east of the cordillera in the Black Hills region of South Dakota (Elmore, 1976; Bailey, 1976; Gelderen, 1994); however, Dorn (1977) reports that the species is not confirmed by a voucher specimen (his or other). Murray (1970) doubts its occurrence, and others ignore it entirely (Bruggen, 1985; Rydberg, 1922). Westward, *A. glabrum* is found in all the major cordillera from the Rocky Mountains to the Pacific coast. The most extreme southwesterly outliers are found in the San Jacinto Mountains of California (Shevock, 1993). In the southern part of its range, *A. glabrum* occurs throughout mountain ranges exceeding 2000 m elevation; in the northwest, throughout the coastal and interior mountain systems from sea level (rarely) to ca. 1500 m elevation.

Reports published in the 19th and early part of this century suggest that both the range and total numbers of *A. glabrum* were somewhat larger than those of today. It is likely that extensive timber harvesting — especially near streams — and the general suppression of broad-leaved species in logged-over areas are factors in the overall reduction in numbers. This change is particularly evident west of the Cascade-Sierra axis in the United States.

Sympatric *Acer* species

Four *Acer* species are sympatric with *A. glabrum*: *A. grandidentatum* Torrey & Gray (bigtooth or canyon maple), *A. circinatum* Pursh (vine maple), *A. macrophyllum* Pursh (bigleaf or Oregon maple) and *A. negundo* L. (boxelder or Manitoba maple). Although there is considerable overlap in the ranges of maples in western North America, actual occurrences of shared habitats are rare. Bigleaf and vine maples are low elevation species, both generally found growing below 1500 m., and Douglas maple (*Acer glabrum* var. *douglasii* [Hooker] Dippel) occasionally shares sites on steep coastal slopes. An entity identified as a possible *A. glabrum* \times *A. circinatum* hybrid was collected in the Fraser River Canyon area by R.L. Taylor and D. Tarrant of the UBC Botanical Garden in 1971. Although the leaves of this specimen are not typical for vine maple at the coast, its axillary buds, twig morphology and leaf vein architecture are consistent with that species and not with those of *A. glabrum*.

Acer negundo var. *interius* (Britton) Sarg. occasionally shares riparian habitats with *A. glabrum* var. *neomexicanum* (Greene) Kearney and Peebles in the southern Rockies. Boxelder trees observed in Boulder, Colorado in *A. glabrum* var. *glabrum* habitat are probably seedlings derived from nearby urban plantings. There is a report of the southeastern North American *A. negundo* var. *violaceum* Booth ex Kirchn. in Idaho (Hitchcock et al., 1961), where it contacts Douglas maple. However, in Idaho, where subsp. *douglasii* was collected in this study, Norway maple (*Acer platanoides* L.) — another "escape" — was the only other maple observed. Bigtooth maple, *A. grandidentatum*, is isolated from Rocky Mountain maple altitudinally where their ranges overlap. The former species occurs at lower elevations, in shady draws, canyon bottoms and ravines. While moisture

requirements would probably be met in these habitats, I suspect that Rocky Mountain maple prefers the cooler temperatures afforded by high elevation. None of these species nor the sections to which they are referred, is considered closely related to Rocky Mountain maple, and there are no known hybrids between them, either artificially produced or naturally occurring (with the possible exception of the entity noted above).

Ecology

To a large degree, maples are microthermal plants (preferring mean annual temperature $<13^{\circ}\text{C}$), favouring humid or subhumid climates (Wolfe, 1987). This is evidenced by their absence from non-fluviatile areas of the steppe, desert and semi-desert, and alpine-tundra areas of western North America. Rocky Mountain maple generally grows on extremely well-drained soils and screes in moist habitats, or in areas where snow melt or mountain streams contribute to soil moisture for at least part of the growing season. In xeric areas, this species inhabits areas near mountain streams, or those receiving appreciable snow and convectional summer rainfall. In the northern parts of the range, plants tolerate considerable sun exposure, but are commonly found as understory plants in coniferous and mixed coniferous-deciduous forests. Under moist, shaded conditions, internode length and ultimate tree height are increased considerably.

Mid-latitude and southern variants are adapted to less mesic conditions, extension growth appearing to be severely limited during droughty periods within the growing season and in dry years, and these plants tend to be shrubby. Sub-riparian and riparian plants are more arborescent, and where there is significant forest cover, tree size approaches that of the northern variants. Plants native to areas with appreciable

convictional rain (generally east of Cascade-Sierra axis) or access to regular moisture, tend to produce relatively more dissected leaves on reproductive shoots than do plants from areas of regular summer drought.

Flowering, Reproduction and Dispersal

The flowering characteristics of maples are diverse. The assumed primitive maples are monoecious, exhibiting duodichogamous flowering (where the flowering sequence is male-female-male). Protogyny is reported to be the most common mode of flowering in maples, and is assumed to be derived from the duodichogamous condition. *Acer glabrum*, however, is reported to have nearly completed the evolution to male trees (Oterdoom & Jong, 1994). According to those authors, *A. glabrum* belongs to a group intermediate between dichogamous and dioecious species. Here, protogynous individuals are partly replaced by female individuals, and protandrous (i.e., duodichogamous) individuals produce only male flowers most years (Oterdoom & Jong, 1994). The species has been characterized as monoecious to dioecious (Torrey, 1828), andromonecious or androdioecious (Ogata, 1967), dioecious (or staminate plants with some bisexual flowers) (Shevock, 1993), or often dioecious (for subsp. *douglasii*) (Gelderen, 1994).

Flowers are assumed to be entomophilous in *A. glabrum*, the trees producing few-flowered corymbs of small, open, yellow, nectariferous flowers, suggesting visits by unspecialized insect pollinators. Primitive sawflies in the genus *Xyela* are reported to feed on the pollen of various dicots, including maple, in western North America (Furniss and Carolin, 1977), and may be responsible for the transfer of pollen in Rocky Mountain maple. Certainly, where Rocky Mountain maple occurs near agricultural areas on

Vancouver Island, honeybees (*Apis mellifera*) collect both nectar and pollen (C. M. Justice, 1994, pers. comm.). On the other hand, the large, exserted stamens in functionally male flowers suggests that these plants may also be wind-pollinated to some degree. In a study of gynoecial development in *Acer*, Peck and Lersten (1991), suggest that the occurrence of papillate stigmas in maples corresponds to increased efficiency in wind pollination, and that this condition may be under-reported in the literature. These authors cite previous work which suggests that there may be some variation in the degree of papillosity within and among *Acer* species. Papillate stigmas are not reported in *A. glabrum*, although Jong (1994) states that *A. glabrum* belongs to a group of maples which manifests various stages of development toward anemophily.

Fruits either follow fertilization of ovules, or develop parthenocarpically with unfertilized ovules. Parthenocarpy is especially common in dioecious maples, and in *A. glabrum* (Oterdoom and Jong, 1994). Sterile and fertile fruits are difficult to differentiate, the nutlet being more or less flattened regardless of the presence of a viable embryo. (Nutlets are rounded in many other species). *Acer glabrum* is known to have a long seed dormancy requirement (Folkerts, 1994, pers. comm; Jong, 1994), germination often occurring in the 2nd or 3rd spring after sowing. Presumably, long seed dormancy ensures the survival of a greater proportion of seedlings in climates with unreliable summer moisture, occasional late killing-frosts, or generally unpredictable weather, conditions common to the mountainous regions of western North America.

Seed of *A. glabrum*, like that of other maple species, is disseminated primarily by wind. Studies on the dispersal of winged fruits have shown that maple samaras are easily dispersed long distances with even low wind velocities (Green, 1980; Greene and

Johnson, 1989). Despite interspecific variation in samara dimensions, terminal velocities (the component of samara flight most responsible for dispersal distance) differ little between species (Guries and Nordheim, 1984). While most trees of Rocky Mountain maple are small relative to other maples, and distances from the fruiting branch to the ground may be modest, Guries and Nordheim (1984) showed that substantial samara dispersal distance can be achieved under light wind conditions even with release from low heights (in maples of similar height). In many parts of its range, *A. glabrum* is typically found in montane environments where wind velocities are commonly high. Rodents and birds may also affect the dispersal of *A. glabrum* seed. Eastern chipmunks are known to collect and cache maple fruits (Price and Jenkins, 1986), thereby distributing seeds, and Elmore (1976) reports that birds, squirrels and chipmunks eat the seeds in the southwest uplands. Bigleaf maple fruits are a major food source for Douglas squirrels on Point Grey (Vancouver, B.C.) (Ganders, 1994, pers. comm.).

Asexual Reproduction

Trees have been observed to be somewhat stoloniferous, especially on unstable slopes where stems become buried for part of their length, perhaps also as a result of repeated browsing. In this way, clonal populations may be built up if adventitious roots arise from buried stems. Some populations sampled for analysis in this study appeared to be made up of colonies of ramets, but this was not investigated further.

Animal Interactions

Maples are common browse plants for ungulates and other mammals in northern

forests (Lee *et al.*, 1990; Chen and Xiao, 1989; Scott *et al.*, 1989; Hughes and Fahey, 1991). Browse damage by moose (Pierce, 1984), elk, deer (Lommasson & Park, 1937; Elmore, 1976; Little, 1985), plains white-tailed and mule deer, and mountain sheep (Van Dersal, 1938) is common in Rocky Mountain maple. With adequate soil moisture during the growing season, basal or sub-basal epicormic growth generally follows such damage — or any damage to shoots — resulting in proliferation of vigorous, erect vegetative shoots, often with ternate leaves (Figure 5.2.2.). Elmore (1976) reports (for the southwest uplands) that birds eat the seeds, buds and flowers of *A. glabrum*.

Round-headed wood borers in the genus *Phymatodes* are known to inhabit both broadleaf and coniferous species throughout western North America (Furniss and Carolin, 1977) and the Holarctic (Cope, 1984). Two closely related species are reported to utilize maples: *A. glabrum* is host to *P. shareeae*, a recently described species in New Mexico (Cope, 1984), and *P. vulneratus* exploits maple and *Fraxinus* species from southern California to British Columbia (Furniss and Carolin, 1977). Foliage gall producing mites are common on many maple species (Pirone, 1960), and Rocky Mountain maple is host to a number of mites. The small, brilliant red galls produced by the eriophyid, *Eriophyes acericola* (or related species) are so conspicuous that they are known in Nuxalk (the language of the Nuxalk [Bella Coola] people of the mid coastal region of British Columbia) as "hummingbird's menstrual pad" (Pojar and MacKinnon, 1994) (Figure 5.2.3.). Other eriophyid mites known to infest *A. glabrum* include the purple erineum maple mite, *E. calaceris*, which causes dense, magenta-coloured, hairlike growths on the undersides of the leaves (Furniss and Carolin, 1977).

Figure 5.2.2. Damaged var. *douglasii* with Basal Shoots



Figure 5.2.3. var. *douglasii* Leaves Infested with Eriophyid Mites



Introgression and Phenotypic Plasticity

Where infraspecific *A. glabrum* taxa overlap, there are often the typical leaf-types of both taxa as well as intermediate forms present. For example, the southernmost populations of var. *torreyi* are in close proximity to populations of var. *diffusum*, and leaf morphology in this area is variable. Hot, dry periods might favour the establishment of var. *diffusum* seedlings here, while cooler, more moist periods might favour var. *torreyi*. Hybrids intermediate in leaf shape between these taxa might subsequently also become established.

Alternatively, or in addition to the above scenario, variation may also reflect a degree of phenotypic plasticity. For example, the wide variation seen in collections — mine and numerous herbarium specimens — may be an artifact of temporal, phenotypic responses to a variable climatic regime. Given a series of droughty years, for example, individuals of var. *torreyi* may reduce overall leaf size, and more resemble var. *diffusum*; similarly, the latter variety may possess the ability to increase leaf size to some degree. Individual leaves in some of my collections are notably larger than those in previous collections from what appear to be precisely the same populations. That my collections were made in a relatively "wet" year probably accounts for the differences.

In a broad area where the ranges of varieties *douglasii* and *glabrum* meet, leaf form is generally intermediate, with a tendency toward the var. *douglasii* "shape". This may reflect introgression to some degree, but I feel that the majority of these plants are simply var. *douglasii* individuals expressing leaf plasticity (i.e., smaller leaves), due to more xeric conditions at the southern limits of its range. Plants here presumably represent Greene's long discarded *A. subserratum*, whose type locality is Lewiston, Idaho.

Taxonomic History

John Torrey published the name *Acer glabrum* in 1828. Subdivision of the species into morphologically and geographically distinctive taxa followed, but there was little agreement by the various authors. For example, regional floras, species circumscriptions and family monographs have differed significantly in their treatments of *A. glabrum*. Ferdinand Pax (1886) recognized 2 species, *A. glabrum* (with var. *tripartitum* [Nutt. ex Torr. & Gray] Pax) and *A. douglasii* Hooker. Pax later submerged *A. douglasii* in *A. glabrum* var. *monophyllum* (Schwërin) Pax, 1902). E.L. Greene took a more liberal view of *A. glabrum* and its constituent taxa. He erected *A. subserratum*, *A. Torreyi*, *A. neo-mexicanum* and *A. diffusum*, and recognized *A. douglasii* and *A. glabrum* (sensu stricto) as segregates (Greene, 1902). F.J. Smiley (1921) reduced Greene's *A. Torreyi* and *A. diffusum* to varietal rank under *A. glabrum*, and reduced *A. bernardinum* Abrams to synonymy under var. *diffusum*.

Allan Keller, working under P.A. Munz at Pomona College Herbarium, investigated previous treatments of *A. glabrum* and prepared a phytogeographic analysis of the species and its constituents (Keller, 1942). Keller published 1 new name, *A. glabrum* var. *greenei* and reduced Greene's *torreyi*, *neo-mexicanum* and *diffusum* to varietal status and his *subserratum* to synonymy with var. *douglasii*. Keller adopted the name *typicum* (subsp. *typicum* Wesmael, 1890) for the type variety.

Edward Murray (1970, 1971, 1975, 1983) is recognized primarily as a prolific *Acer* nomenclaturalist whose forays into taxonomic rearrangement have met with some resistance (his classification of Aceraceae is non-phylogenetic, for example), especially with respect to the utility of his infraspecific taxa (Delendick, 1981, p. 35). Murray has

made a number of combinations for *A. glabrum* segregates, including: elevating to subspecific rank the varieties *neomexicanum*, *torreyi* and *diffusum*, as well as erecting the subspecies *siskiyouense*. The most recent treatment of *A. glabrum* is in the comprehensive *Maples of the World* (Gelderen *et al.*, 1994). This treatise is considered the most authoritative analysis of the genus to date. The names for infraspecific taxa accepted in that volume are listed in Table 5.2.1.

Table 5.2.1. Infraspecific *A. glabrum* Taxa Recognized in Gelderen *et al.* (1994)

subsp. *glabrum*

subsp. *diffusum* (Greene) E. Murray (1971)

subsp. *douglasii* (Hook.) Wesmael (1890)

subsp. *neomexicanum* (Greene) E. Murray (1970)

subsp. *siskiyouense* E. Murray (1983)

var. *greenei* Keller (1942)

var. *torreyi* (Greene) Smiley (1921)

forma *bicolour* Pax (1886)

5.3. *Acer glabrum* Intraspecific Taxa

Taxonomic Criteria

The retention of the rank of *varietas* (variety) for the intraspecific taxa studied here is based upon a number of factors. While the intraspecific taxa all differ morphologically, and these differences appear to be genetically determined to some degree (as evidenced by transplant trials), conspicuous differences beyond leaf shape variation are few. *Acer glabrum* segregates are largely allopatric, but areas of overlap are extensive in certain areas where intermediates (presumed hybrids) are common.

With few amendments, the system put forward by Allan Keller in 1942 adequately represents the geographic variation in the species. About the taxonomic criteria used in assigning rank to these segregates, Keller wrote: "Since no constant differentiating features have been discovered in floral or fruit morphology and since the only differences observed have been those of leaf-size -shape and -division and twig color, it seemed best to consider these minor and rather variable differences as worthy of varietal rank only. Furthermore, each entity ... has a fairly definite geographical range with considerable intergradation where their ranges overlap." Clearly, very little taxonomically important information has been added to our body of knowledge about this species since Keller's circumscription.

In light of our ignorance of the developmental biology and population genetics of this species, the lack of evidence that there is a need for more than a single intraspecific category, and the fact that there are perfectly adequate varietal names for all of the geographical segregates, it would seem unnecessary to elevate any of these names to the

rank of subspecies. When and if unequivocal information comes to light establishing that a subset of *A. glabrum* varieties forms a monophyletic group, a higher infraspecific category, i.e., the rank of subspecies, would then be appropriate.

Table 5.3.1. Key to the Intraspecific Taxa of *Acer glabrum*

- 1a. Leaves mostly > 3 cm across, 4° veins visible
 beneath. 2.
- 1b. Leaves mostly < 3 cm across, 4° veins not visible
 beneath. Utah, Nevada, California var. *diffusum*
- 2a. Leaves from non-extension shoots 3-5-lobed, or if 3-
 parted, then < 6 cm across and not glaucous
 beneath 3.
- 2b. Leaves from non-extension shoots 3-parted or nearly
 so, > 6 cm across, glaucous beneath. New Mexico,
 Colorado, Utah, Arizona var. *neomexicanum*
- 3a. Leaf lobes and marginal teeth usually acute, marginal
 teeth often > 4mm, 4° and 5° veins clearly visible,
 areole development good 4.
- 3b. Leaf lobes and marginal teeth usually broad and apically
 rounded, marginal teeth < 4 mm, 4° and 5° veins
 somewhat obscured, areole development poor.
 Oregon, California, Nevada var. *torreyi*
- 4a. Leaves from non-extension shoots 3-5-lobed, < 6 cm
 across; 3° and 4° veins usually reticulate. Idaho,
 Wyoming, Colorado, Arizona, Nebraska, Utah var. *glabrum*
- 4b. Leaves from non-extension shoots 3-5-lobed, > 6 cm
 across; 3° and 4° veins orthogonal. Alaska,
 Alberta, BC, Montana, Idaho, Washington, Oregon var. *douglasii*

A. glabrum var. *glabrum*.

A. glabrum subsp. *typicum* Wesmael, Bull. Soc. Belgique 29: 46 (1890). *A. glabrum* forma *monophyllum* Schwerin, Gartenfl. 42: 650 (1893). *A. glabrum* var. *typicum* (Wesmael) Keller, Amer. Midl. Nat. 27: 493 (1942).

Type: Dr. James, in the Rocky Mountains about latitude 40 degrees (holotype: NY).

A. tripartitum Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 247 (1840).

A. glabrum var. *tripartitum* (Nutt. ex Torr. & Gray) Pax, Bot. Jahrb. 7: 218 (1886).

A. glabrum forma *tripartitum* (Nutt. ex Torr. & Gray) Schwerin, Gartenfl. 42: 650 (1893). *A. glabrum* forma *trisectum* Sargent, Jour. Arnold Arb. 2: 166 (1921).

Type: Nuttall, On Bear Ridge, Rocky Mountains, latitude 40 degrees, near the line of Upper California (holotype: NY).

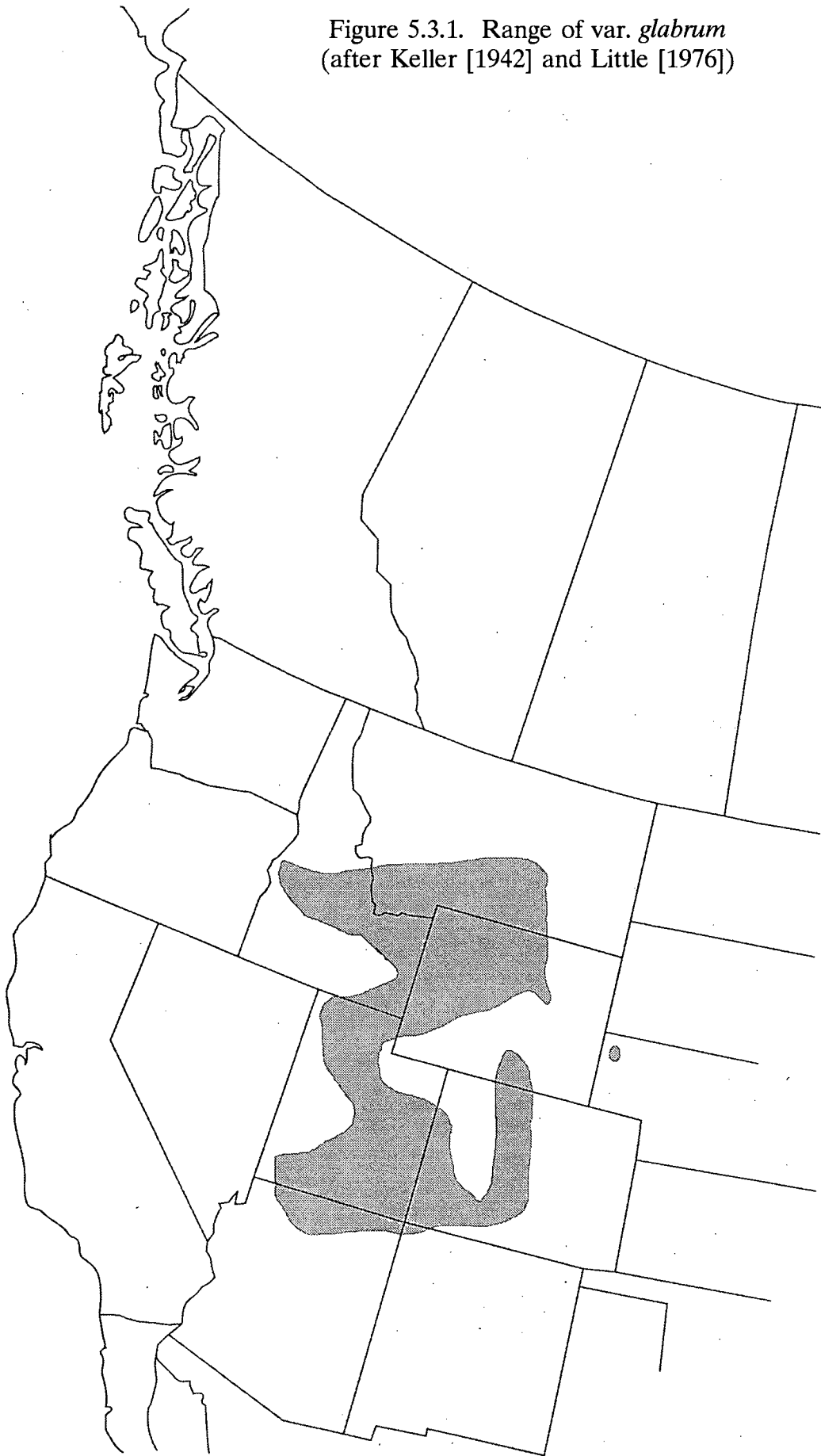
A. glabrum subsp. *neo-mexicanum* var. *parvifolium* E. Murray, Kalmia 11: 4 (1981).

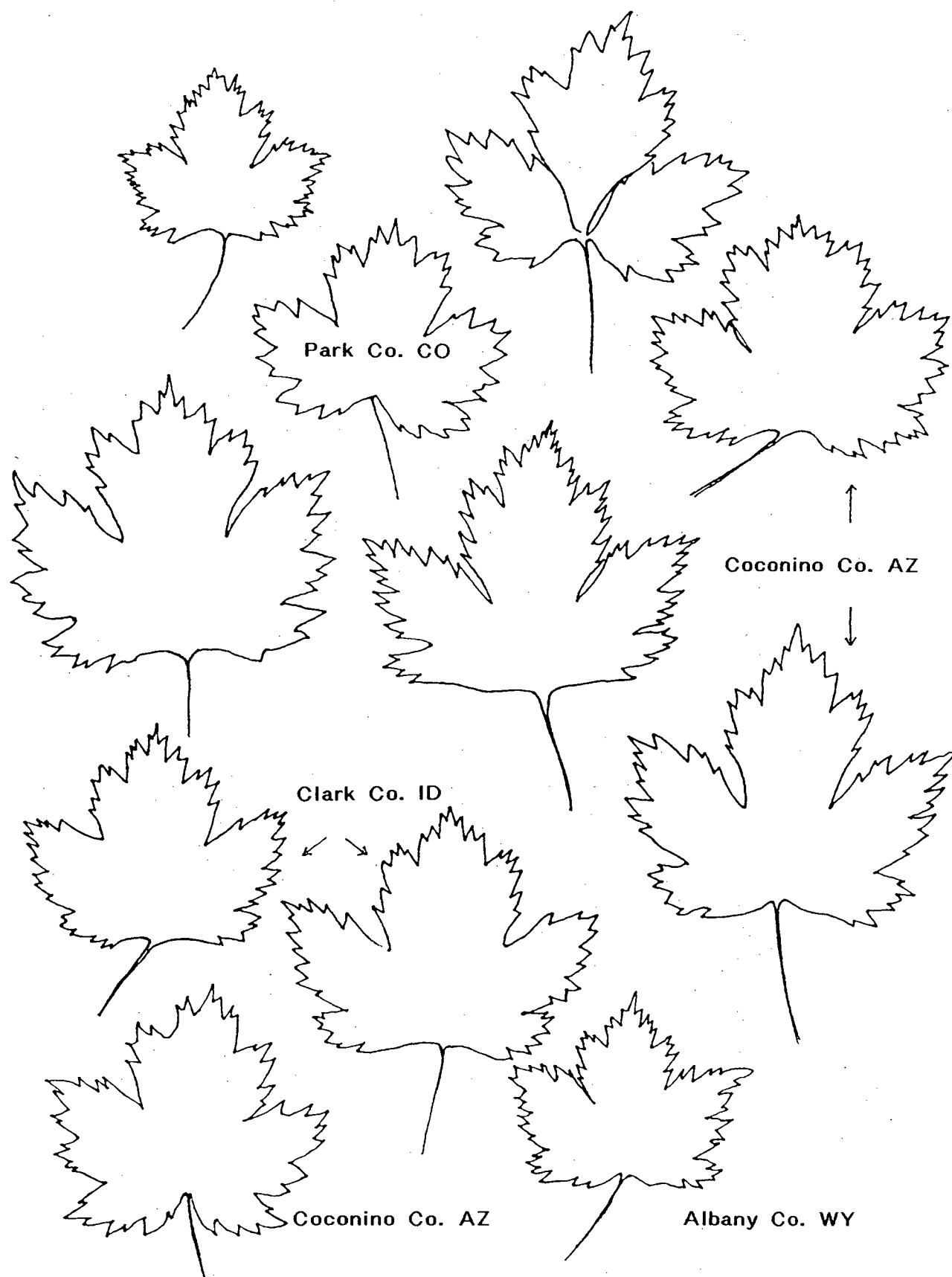
Type: J. & C. Taylor 8726, 10 mi. E of Shell, in Shell Canyon, Big Horn County, WY (holotype: DUR).

Plants shrubby to tree-like, 3-8m; twigs reddish or greyish. Leaves 3-5-lobed, often 3-parted on extension growth and especially on epicormic shoots, 4-6 cm across with acute lobes and prominent marginal teeth; 4th order veins visible beneath, reticulate; areole development poor. Figures 5.3.1. and 5.3.2. Herbarium specimens examined are listed in Appendix 1.

Variety *glabrum* occurs on steep slopes and mountainsides along streams and in snow catchment areas, at elevations between 1500 and 2500 m in the central and southern Rockies and in the mountains of the eastern Great Basin (Rocky Mountain Province).

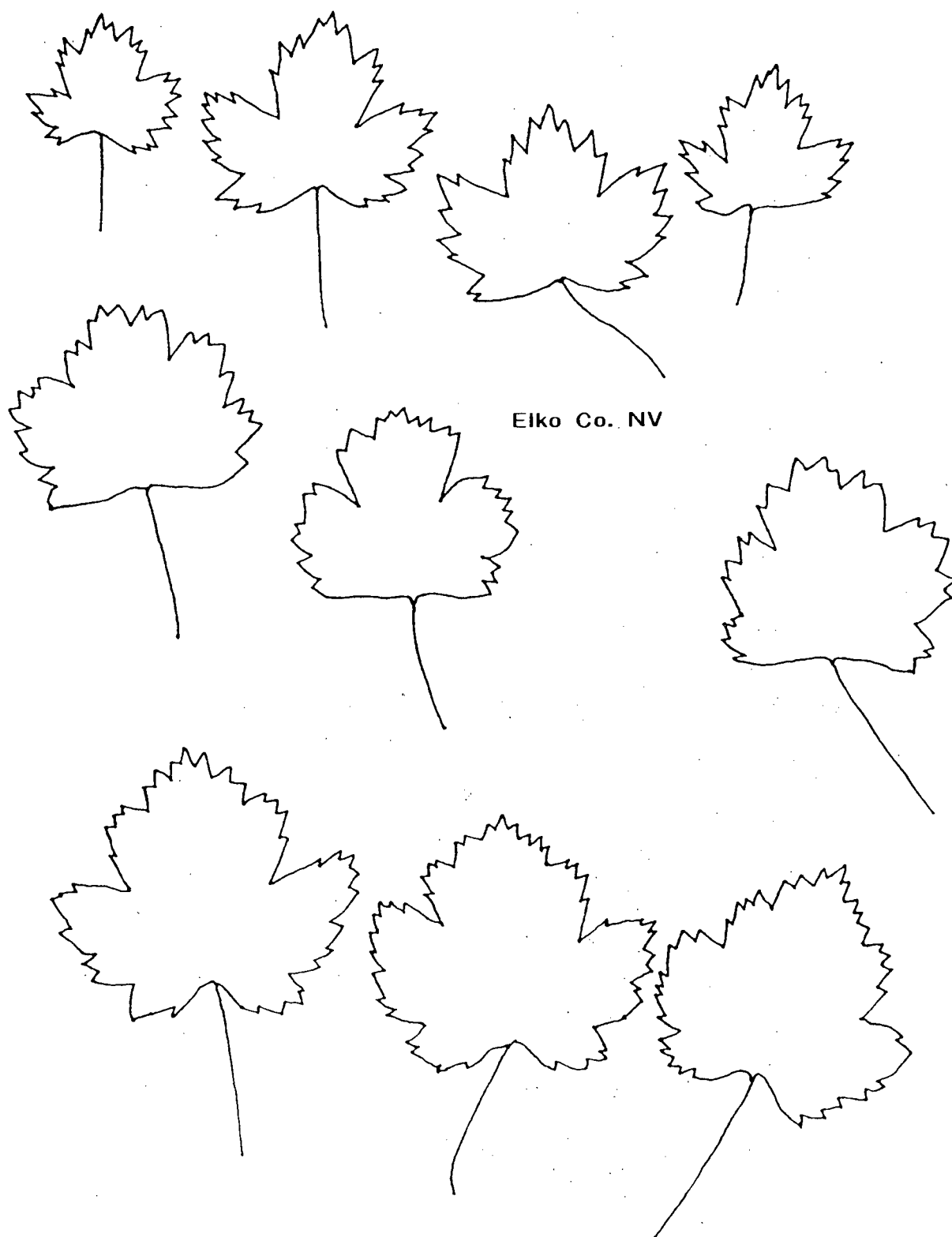
Figure 5.3.1. Range of var. *glabrum*
(after Keller [1942] and Little [1976])

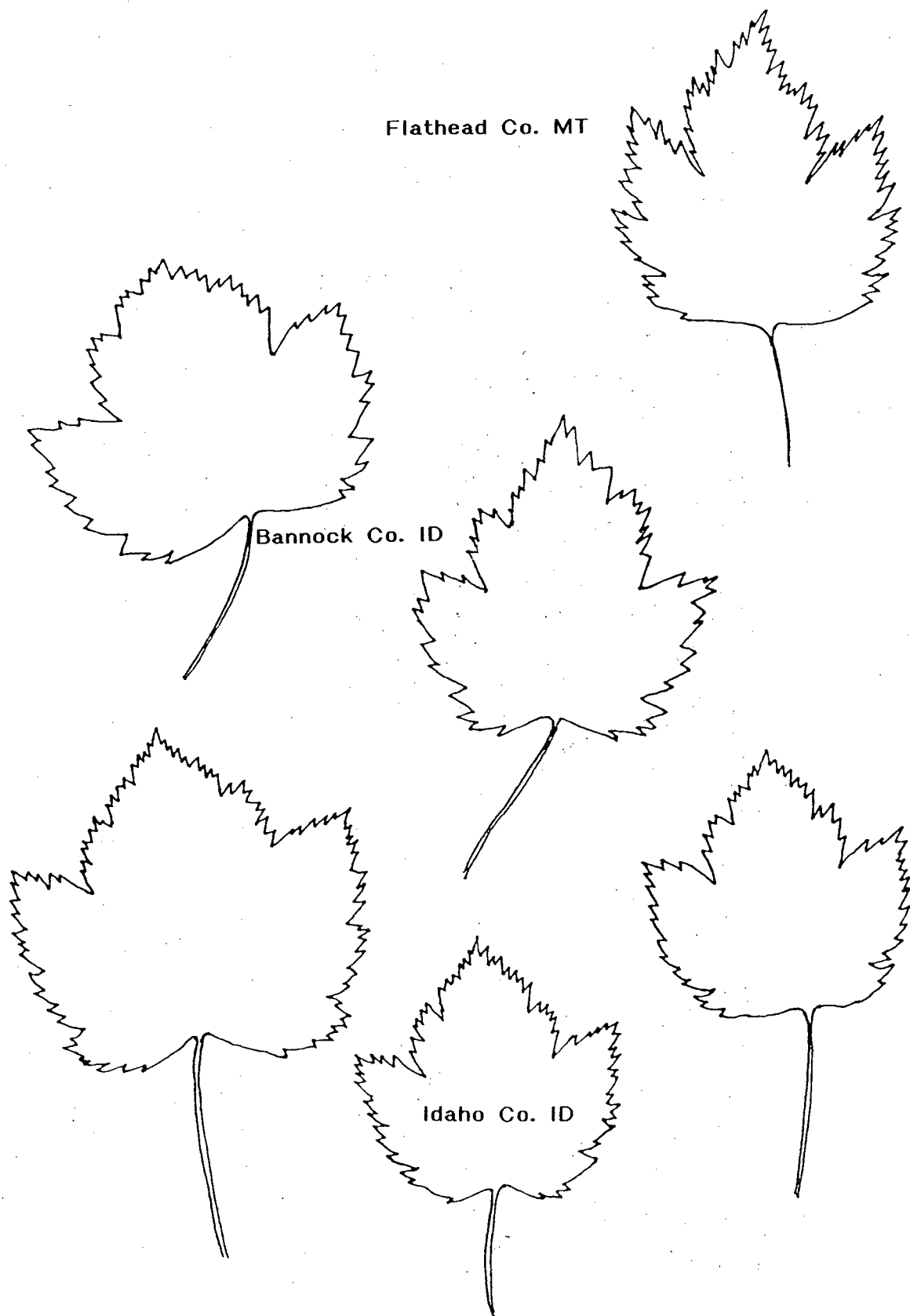


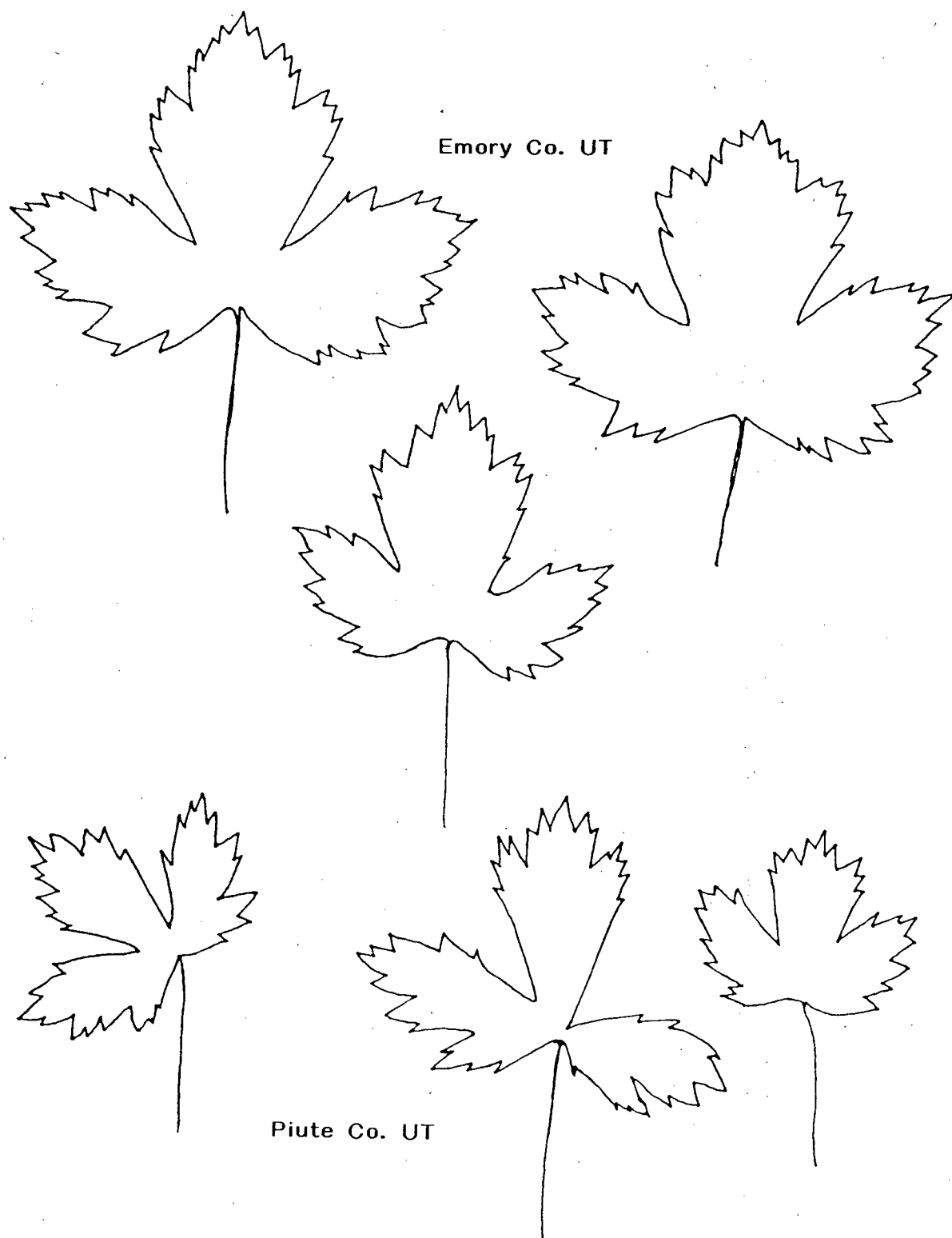


Reported in Wyoming, Colorado, Idaho, Utah and northern Arizona. A disjunctive population is reported to occur in northwestern Nebraska (Little, 1976; McGregor et al., 1986). Variety *glabrum* intergrades to the west on the mountainous fringes of the eastern Great Basin with var. *diffusum* (Figure 5.3.3.), to the north in Idaho and Wyoming with var. *douglasii* (Figure 5.3.4.), and with var. *neomexicanum* (Figure 5.3.5.) in New Mexico, Arizona and Utah to the south and west. This variety is associated with Douglas fir-lodgepole pine and fir-spruce forests in the montane and subalpine zones.

Variety *tripartitum*, a name in limited use today, is considered an ecad and is assigned to var. *glabrum*. The epithet *tripartitum* was coined by Torrey and Gray (1840) for plants with small, ternate leaves collected by Nuttall in the Central (US) Rockies. However, this name was later appropriated by Pax (1886) to differentiate the deeply dissected to ternate forms from the less-dissected forms (those forms united under *A. glabrum* var. *monophyllum*). Keller (1942) resurrected the epithet for use in its originally intended sense. Unfortunately, there is little to separate Nuttall's plant from others of var. *glabrum*, in that the appearance of ternate leaves is merely *more prevalent* in the type locality of var. *tripartitum*, and *less prevalent* in the type locality of var. *glabrum*.







A. glabrum var. *diffusum* (Greene) F. Smiley, Univ. Calif., Pub. Bot. 9: 261 (1921).

A. diffusum Greene, Pittonia 5: 2 (1902). *A. bernardinum* Abrams, Torreyia

7: 219 (1907). *A. glabrum* subsp. *diffusum* (Greene) E. Murray, Kalmia 3: 14 (1971b).

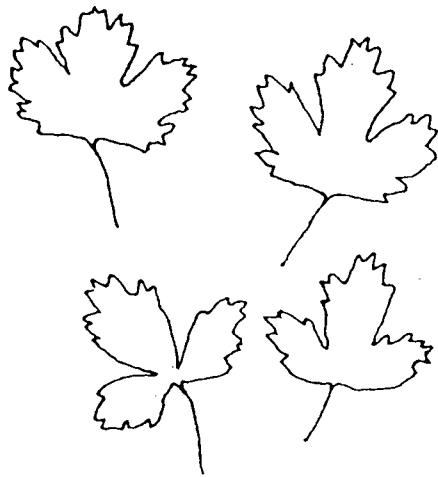
Type: Greene, 1895, Humboldt Mountains, NV (holotype: ND).

Plants shrubby, <4m; twigs whitish. Leaves usually < 3 cm wide, 3-5-lobed or occasionally 3-parted, with few blunt marginal teeth; 3rd and higher-order veins obscured beneath. Figures 5.3.6. and 5.3.7. Herbarium specimens examined are listed in Appendix 1.

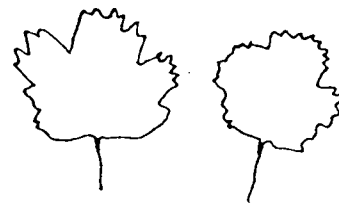
Acer glabrum var. *diffusum* grows on steep slopes at between 2000-3000 m elev. in snow catchments and near streams in the mountains of the western Great Basin (Great Basin Province) and the desert mountains of southeastern California (California Desert Province [Shevock, 1993]), and into the San Jacinto mountains of southwestern California (Californian Province). Variety *diffusum* is reported in Nevada, southwestern Utah, northwestern Arizona and eastern and southwestern California. This variety intergrades with var. *neomexicanum* (Figure 5.3.8.) in southwestern Utah and northwestern Arizona, with var. *glabrum* (Figure 5.3.3.) in northern Utah, and with var. *torreyi* (Figure 5.3.9.), in the eastern Sierra. This variety is primarily associated with White fir-Pinyon Woodland (Thorne, 1982).

Figure 5.3.6. Range of var. *diffusum*
(after Keller [1942] and Little [1976])

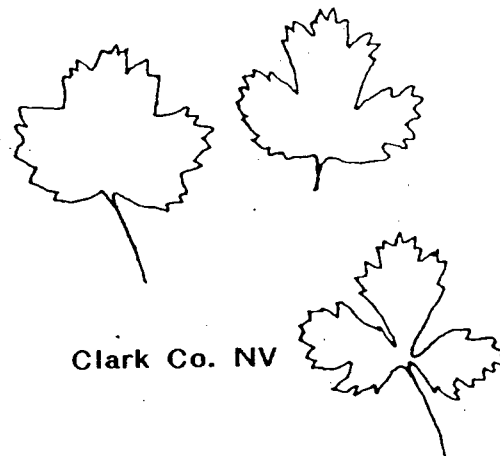




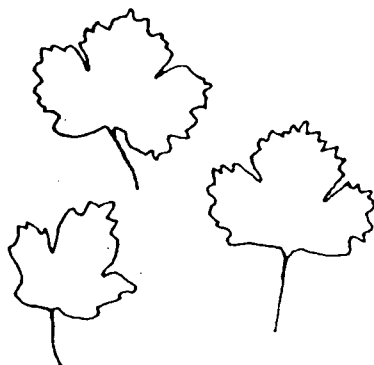
White Pine Co. NV



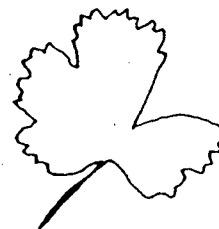
Nye Co. NV



Clark Co. NV



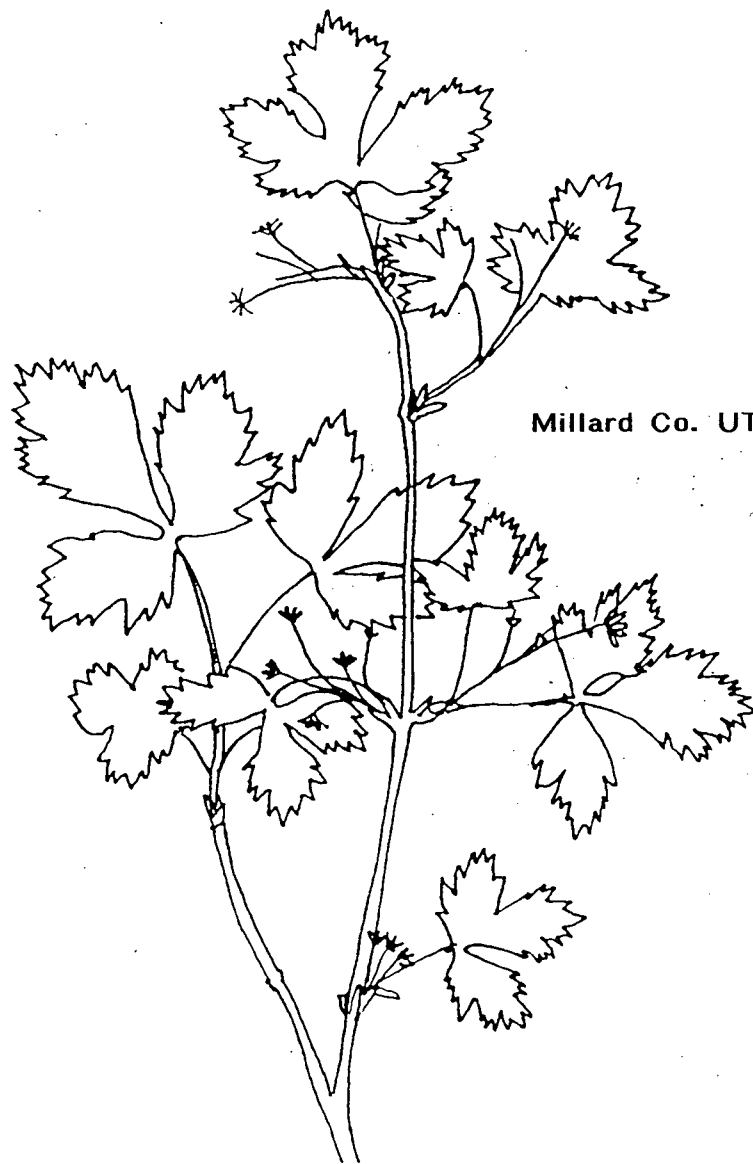
San Bernardino Co. CA

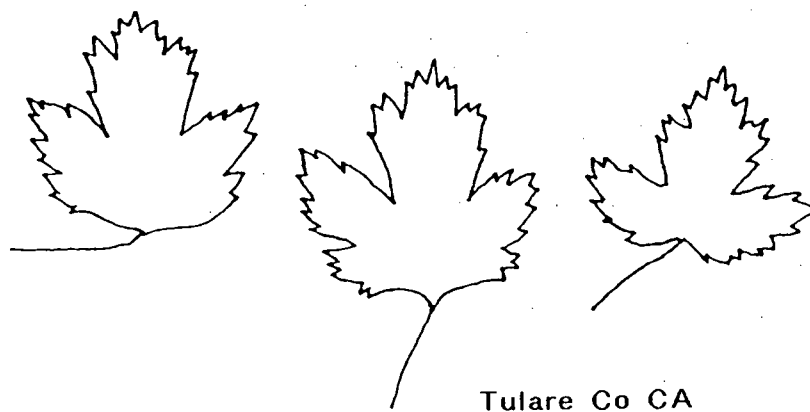
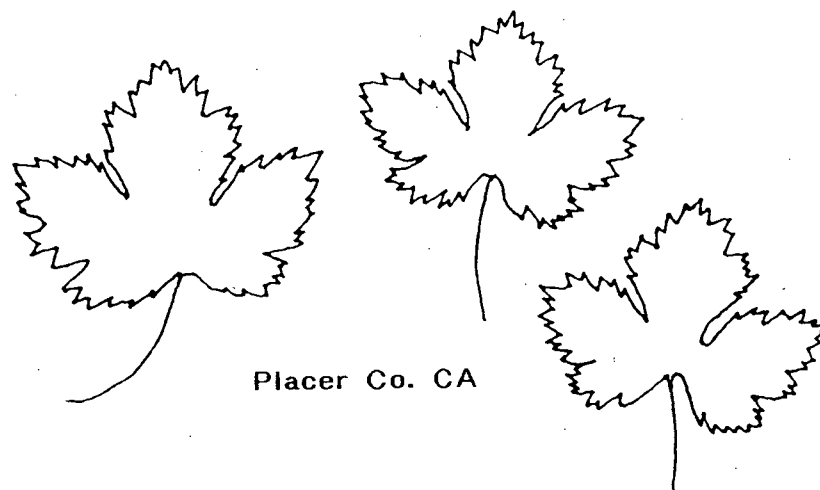


Inyo Co. CA



San Jacinto Mtns CA





A. glabrum var. *douglasii* (Hook) Dippel, Handb. Laubholzkunde 2: 438 (1892).

A. douglasii Hook., London Jour. Bot. 6: 77, pl. 6 (1847). *A. barbatum* Hook., Fl. Bor. Amer. 1: 113 (1831), not of Michx. (1803). *A. glabrum* subsp. *douglasii* (Hook.) Wesmael, Bull. Soc. Belgique 29: 46 (1890). *A. glabrum* var. *monophyllum* (Schwerin) Pax, Pflanzenr. IV 163: 45 (1902).

Type: unknown (Syntypes: K).

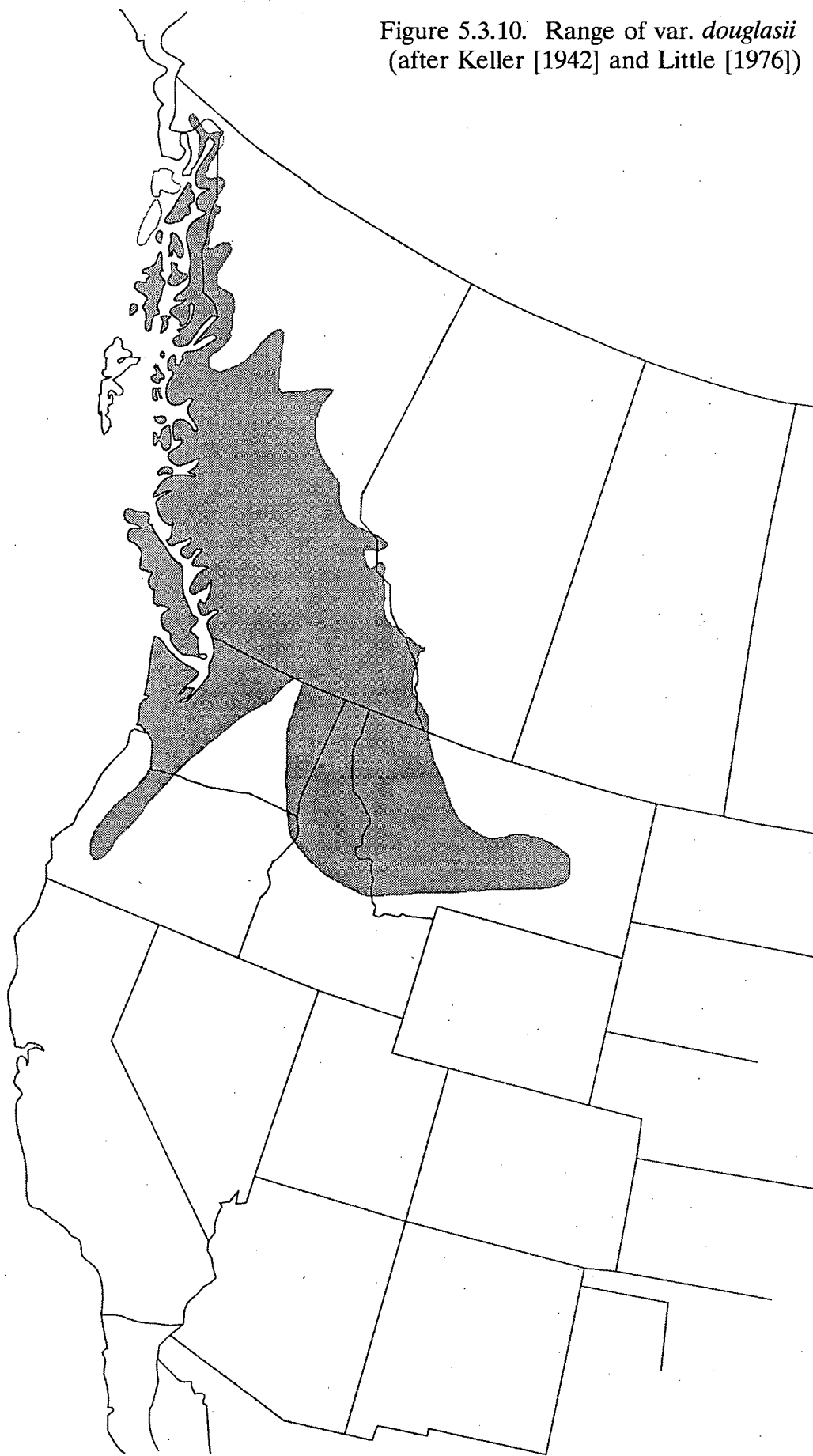
A. subserratum Greene, Pittonia 5: 2 (1902).

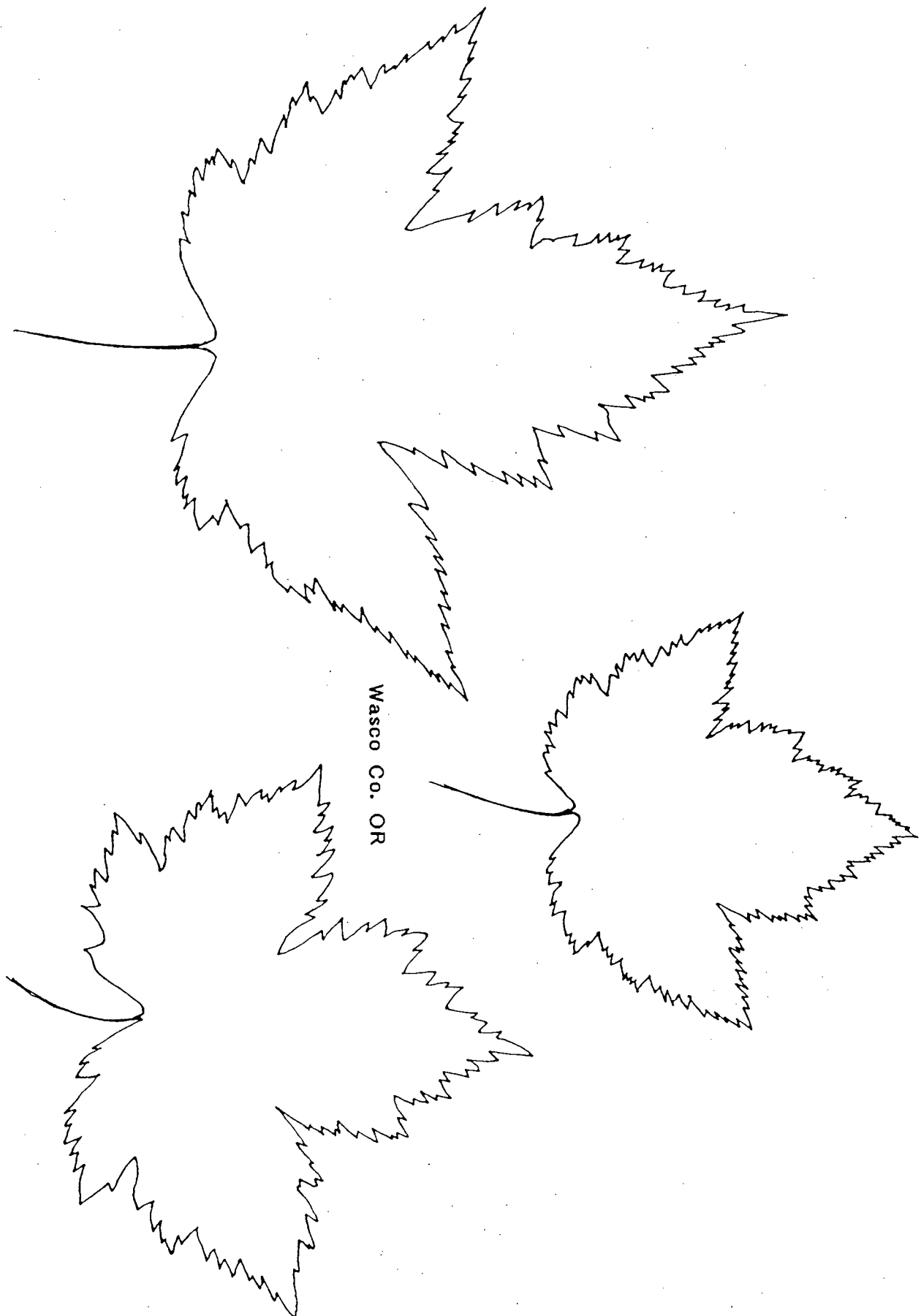
Type: Heller 3089, *Lewiston, Idaho* (holotype?: C, NY).

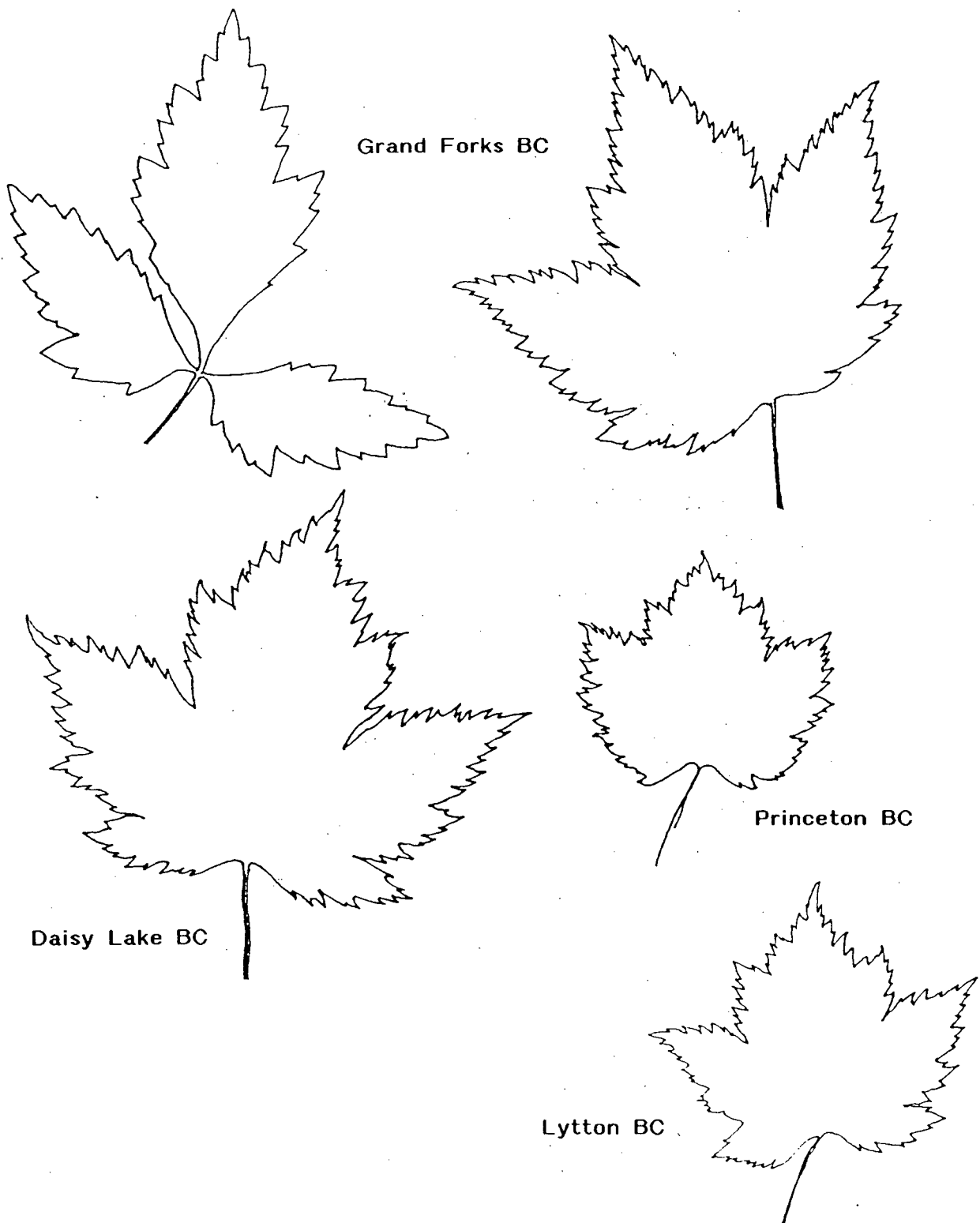
Plants shrubby to tree-like, 2-15m, often fastigate; twigs reddish or (in shade) greyish. Leaves 3-5-lobed, 6-12(-20) cm across, usually with barely acute lobes and shallow sinuses, and with mostly doubly-serrate, prominent marginal teeth; 3rd and 4th-order veins clearly visible beneath, orthogonal; areoles well-developed. Figures 5.3.10. and 5.3.11. Herbarium specimens examined are listed in Appendix 1.

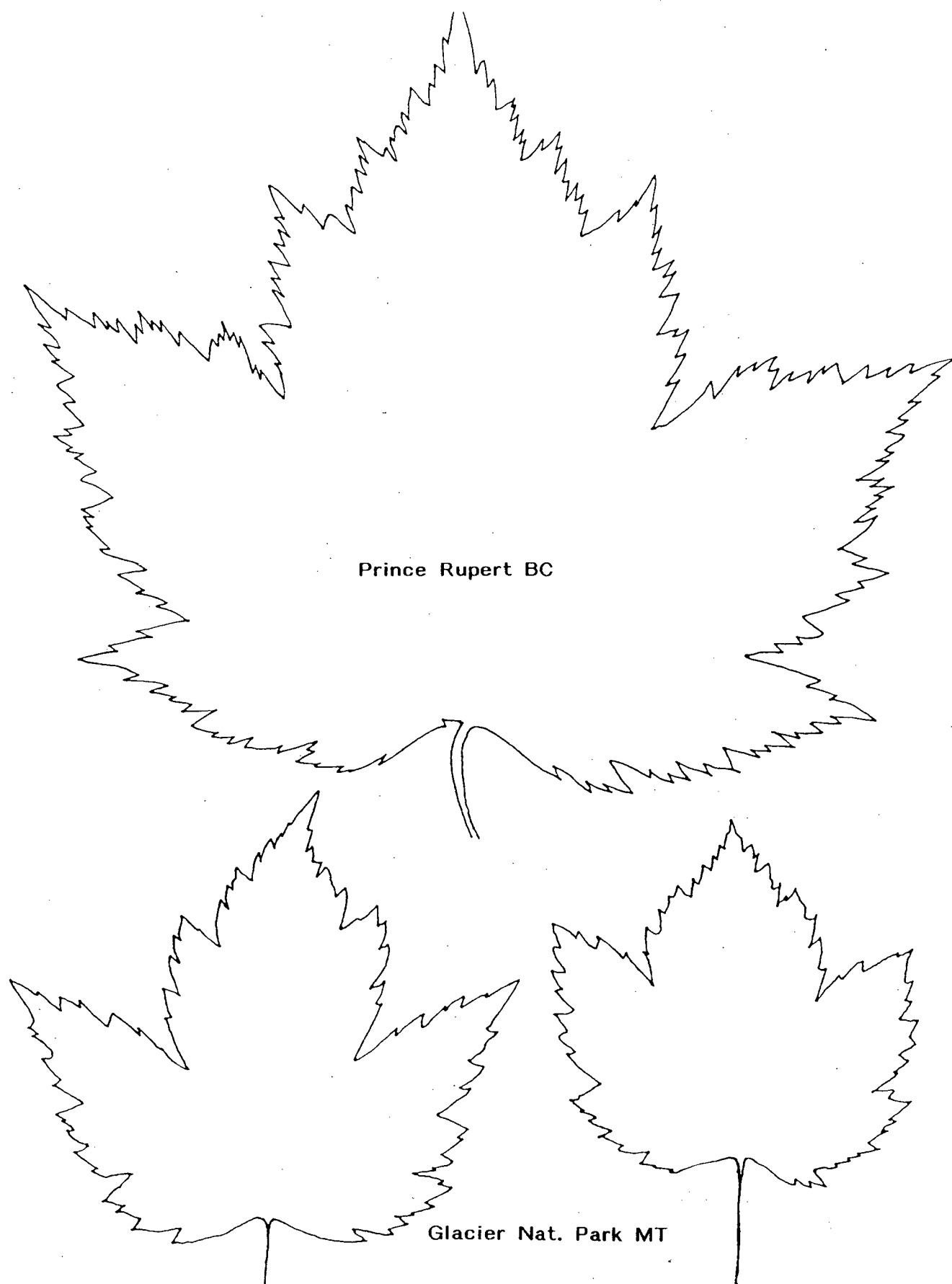
Douglas maple (*A. glabrum* var. *douglasii*) is found on steep slopes and mountainsides up to 2000 m, and rarely in coastal lowlands. It occurs in southeastern Alaska, central and southern British Columbia, southwestern Alberta, western Montana, Idaho, Washington and Oregon. In the west, i.e., the Vancouverian Province (Takhtajan, 1986) (Figure 5.2.1.), it occurs only very rarely in the Coastal Douglas Fir (Gulf Islands subzone) and rarely in the Coastal Western Hemlock Biogeoclimatic Zones of British Columbia (Krajina, 1965, 1969). In the Pacific Northwest states, Douglas maple grows in the Puget Sound area (Kruckeberg, 1982) of the *Tsuga heterophylla* Vegetation Zone

Figure 5.3.10. Range of var. *douglasii*
(after Keller [1942] and Little [1976])









(Franklin & Dyrness, 1973) (referable to the Coastal Western Hemlock Dry Biogeoclimatic Subzone [Krajina, 1965, 1969]). In the east, i.e., the Rocky Mountain Province (Takhtajan, 1986) (Figure 5.2.1.), it occurs in the *Pinus ponderosa*, *Abies lasiocarpa* and *Abies concolor* Vegetation Zones of eastern Washington and Oregon (east of the Cascade crest) (Franklin & Dyrness, 1973); in British Columbia east of the Cascades and in the central part of the province, Douglas maple grows in the following Zones: Interior Douglas Fir; Interior Western Hemlock; Ponderosa Pine-Bunchgrass; Cariboo Aspen-Lodgepole Pine-Douglas Fir; Sub-boreal Spruce; Engelmann Spruce-subalpine Fir (Krajina, 1965, 1969).

In the northern Rocky Mountain states, Douglas maple is a montane to subalpine element in douglas fir-pine and fir-spruce forests. As habitats become drier and less densely forested to the south, var. *douglasii* intergrades with var. *glabrum* (Figure 5.3.4.) in Idaho and Montana. In the west, var. *douglasii* presumably intergrades with var. *torreyi* in Oregon.

A. glabrum var. *neomexicanum* (Greene) Kearey & Peebles, Jour. Wash. Acad. Sci. 29: 486 (1939).

A. neo-mexicanum Greene, Pittonia 5: 3 (1902). *A. glabrum* var. *tripartitum* (Nutt. ex Torr. & Gray) Pax, Bot. Jahrb. 7: 218 (1886). *A. glabrum* subsp. *neo-mexicanum* (Greene) E. Murray, Kalmia 2: 1 (1970).

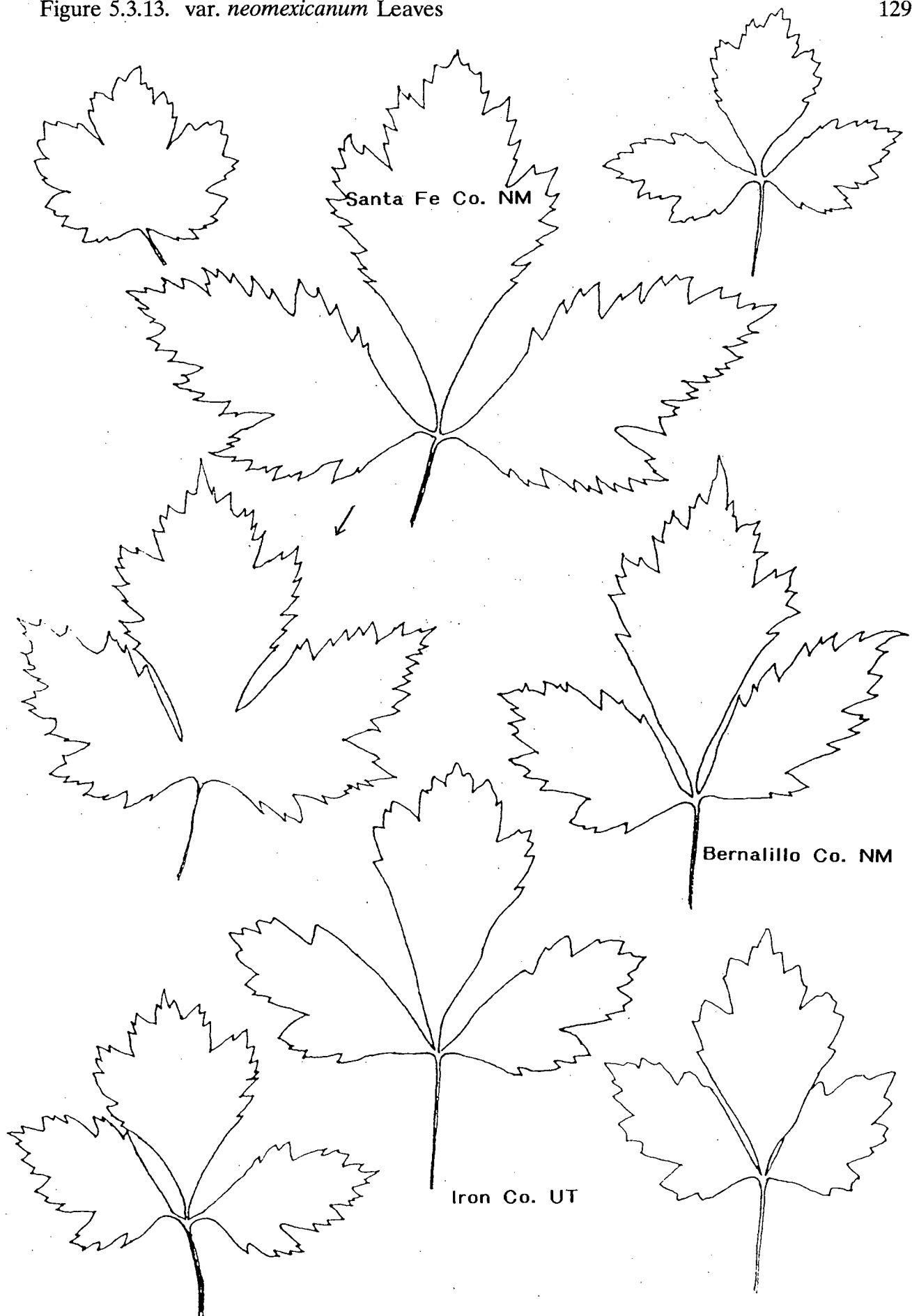
Type: Vasey, 1881, Las Vegas, NM (lectotype: US).

Plants shrubby to tree-like, 3-8m; twigs reddish. Leaves 5-10 cm across, mostly 3-parted, or nearly so, with prominent marginal teeth, often glaucous beneath; 4th-order veins visible beneath, orthogonal or reticulate; areoles well-developed. Figures 5.3.12. and 5.3.13. Herbarium specimens examined are listed in Appendix 1.

Growing on steep slopes 2000-3000 m elev. in snow catchments or near streams. The range of var. *neomexicanum* occurs in the southernmost part of the Rocky Mountain Province, in southern Colorado, New Mexico, southern Utah and southeastern Arizona. Variety *neomexicanum* intergrades with var. *diffusum* (Figure 5.3.8.) in southwestern Utah and northwestern Arizona, with var. *glabrum* (Figure 5.3.5.) in northern New Mexico and Arizona and southern Utah and Colorado. It is marginally abundant in Douglas fir-white fir and subalpine fir-spruce forests.

Figure 5.3.12. Range of var. *neomexicanum*
(after Keller [1942] and Little [1976])





A. glabrum var. *torreyi* (Greene) Smiley, Univ. Calif., Pub. Bot. 9: 261 (1921).

A. Torreyi Greene, Pittonia 5: 2 (1902). *A. glabrum* var. *greeni* Keller, Amer.

Midl. Nat. 27: 500 (1942). *A. glabrum* subsp. *torreyi* (Greene) E. Murray, Kalmia 3: 14 (1971).

Type: no type cited.

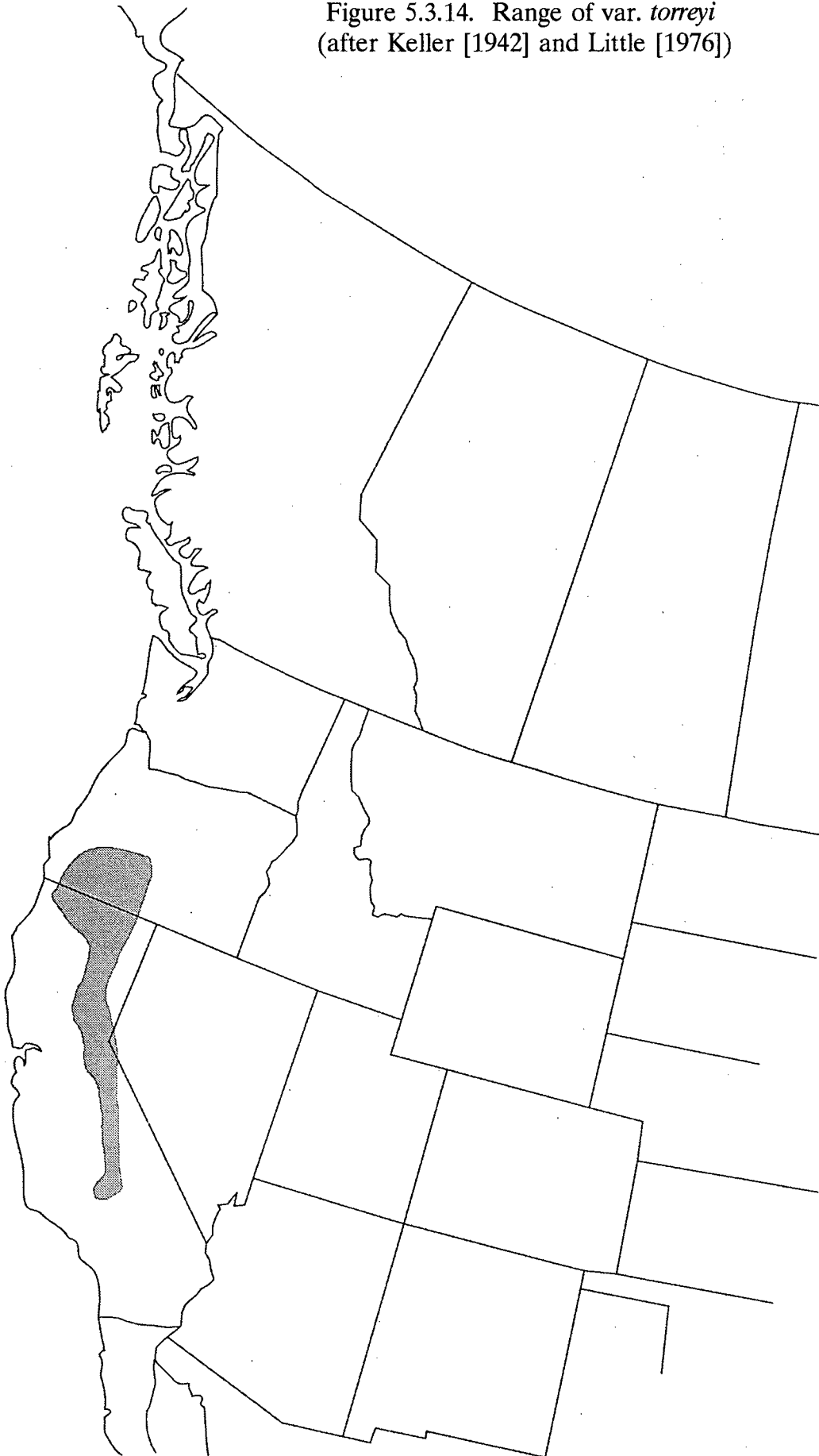
A. glabrum subsp. *siskiyouense* E. Murray, Kalmia 13: 3 (1983).

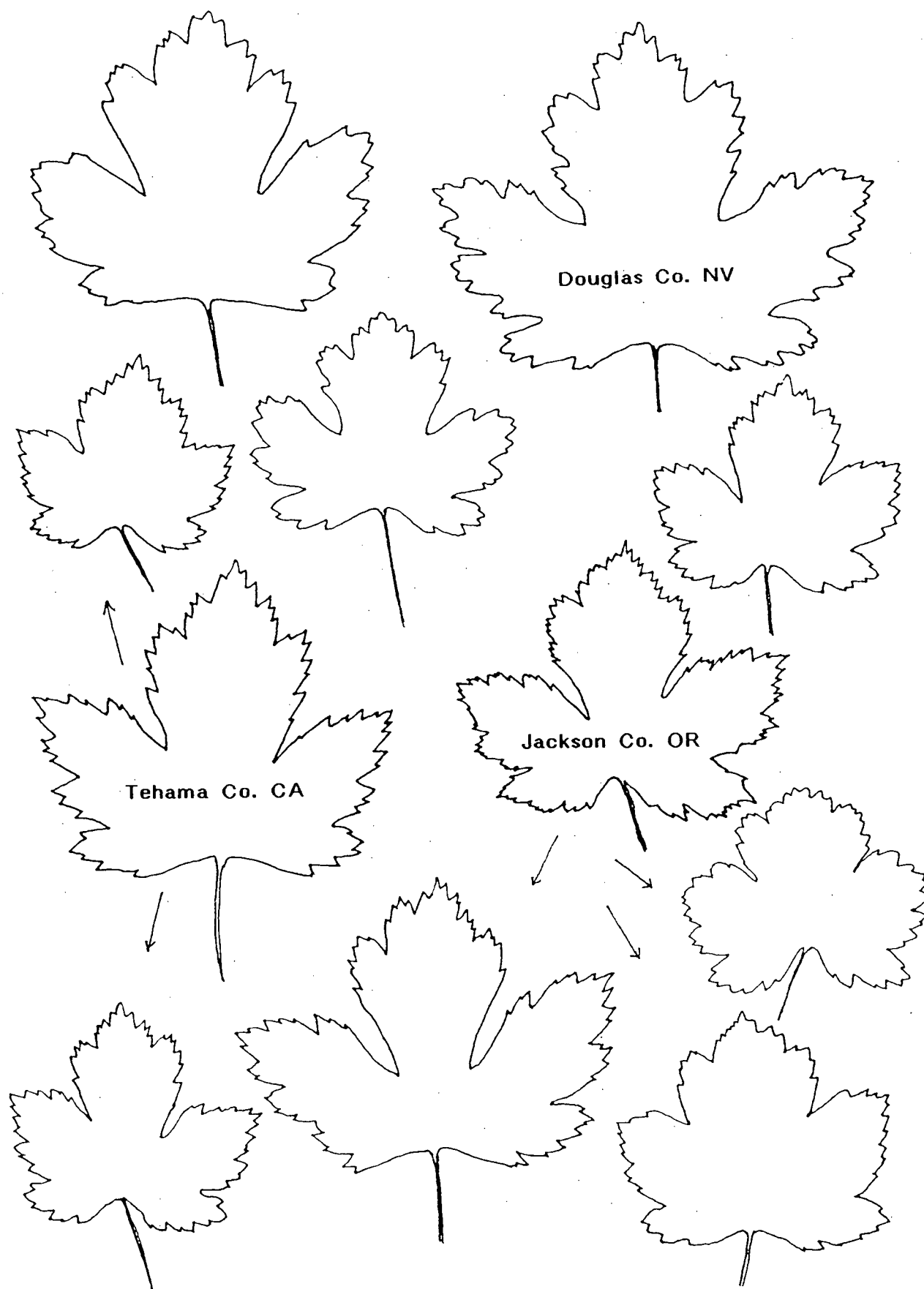
Type: Alexander & Kellogg 5599, *Top of grade between Sawyers Bar and Etna, Altitude 5700', Siskiyou County CA* (holotype: UC).

Plants shrubby to tree-like, 3-6m; twigs reddish. Leaves 3-5-lobed, 4-6 cm across, usually with deep, narrow sinuses, lobes often rhomboidal and usually apically rounded in outline, and usually with blunt marginal teeth; higher-order veins somewhat obscured beneath. Figures 5.3.14. and 5.3.15. Herbarium specimens examined are listed in Appendix 1.

A. glabrum var. *torreyi*, or Sierra maple, is a common shrubby tree in the interior mountains of California, southeastern Oregon and western Nevada, growing on steep slopes 1500-2500 m elev. in snow catchments or near streams. It occurs in the Klamath - Siskiyou and Cascade Ranges and the High Sierra Nevada (Californian Province [Shevock, 1993]) and the Modoc Plateau of northeastern California and extreme western Nevada (Great Basin Province, Madrean Floristic Region [Takhtajan, 1986]) (Figures 1.1.2.) in fir-pine forests (distribution from Shevock, 1993). Leaf morphology of "var. *torreyi*" plants from the Great Basin Province, i.e., east and south of the Sierra Nevada, is intermediate between varieties *diffusum* and *torreyi* (Figure 5.3.9.). and either reflects introgression or phenotypic plasticity. Presumably, var. *torreyi* intergrades with

Figure 5.3.14. Range of var. *torreyi*
(after Keller [1942] and Little [1976])





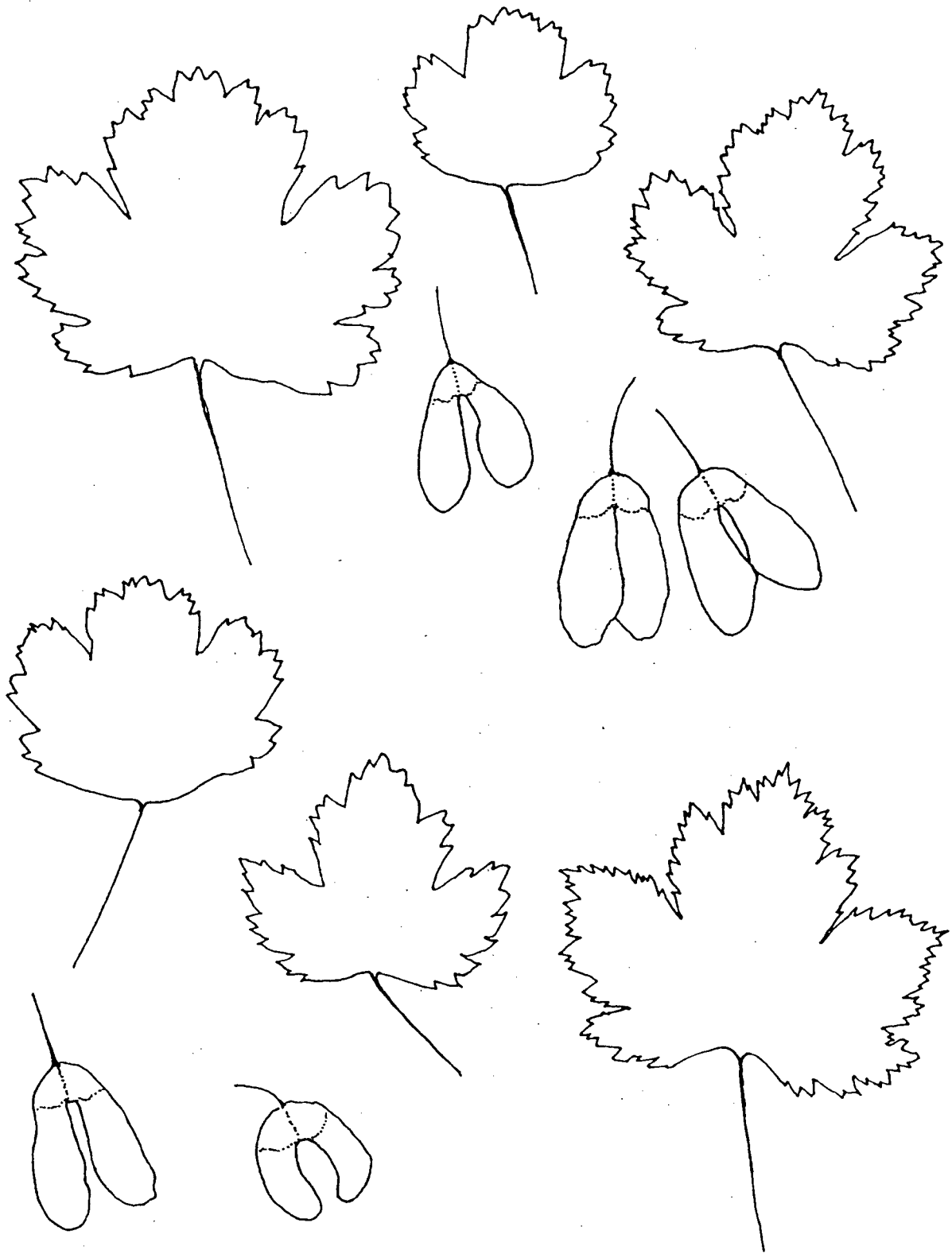
var. *douglasii* in Oregon; however, no such foliar material was seen in this study.

No type specimen was cited in Greene's original description of *A. torreyi* (1902), nor has the taxon been lectotypified. Time constraints have unfortunately prevented me from correcting this situation before completion of this thesis.

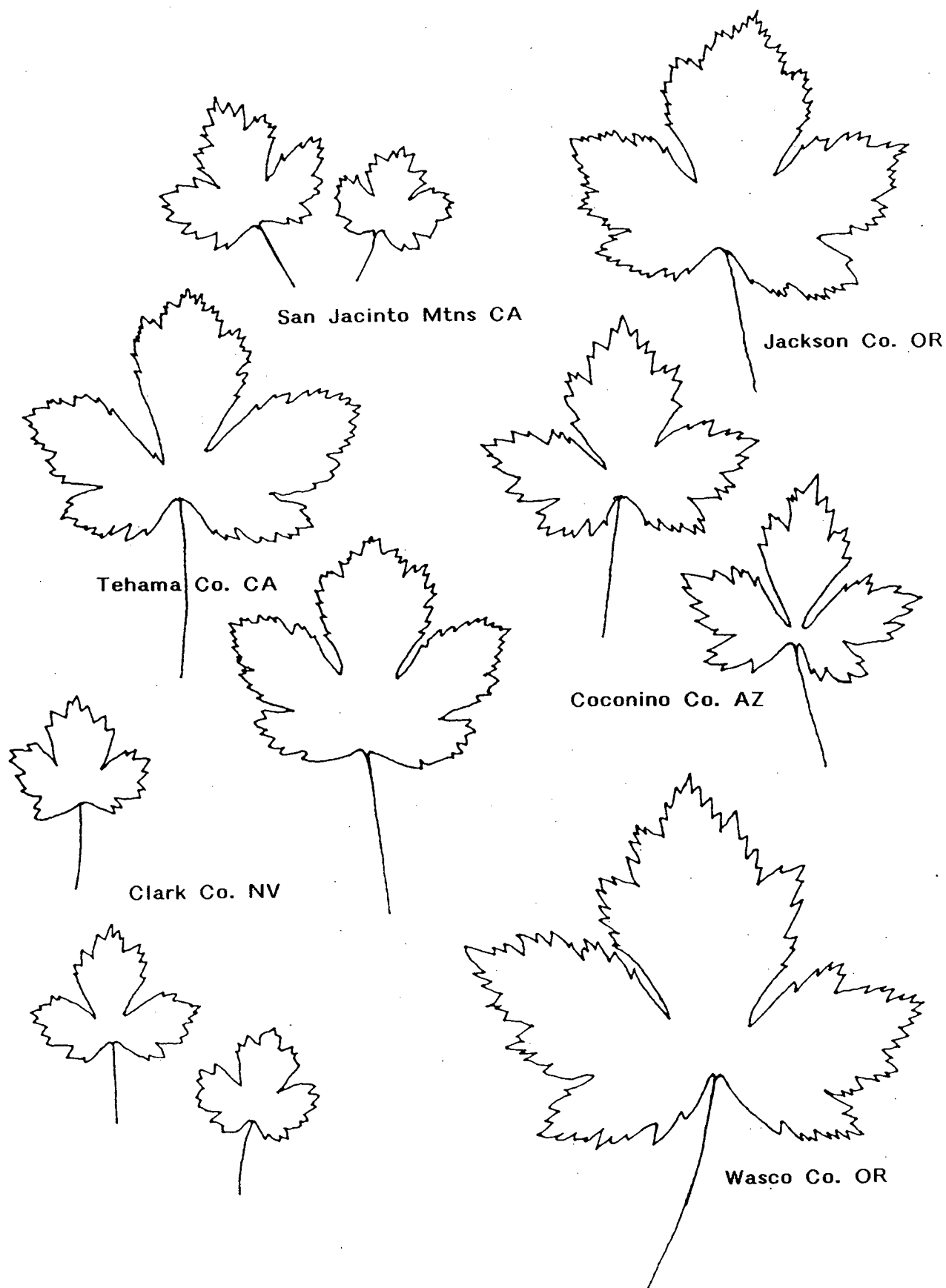
Rejected names in current usage are var. *greenei* and subsp. *siskiyouense*, both here referred to var. *torreyi*. The defining characters in both of these entities are neither constant within supposed taxon localities, nor confined to those localities.

Keller (1942) describes *A. glabrum* var. *greenei* as "most nearly resembl[ing] *Torreyi*, although some specimens are somewhat like those of var. *diffusum*". According to Keller (1942), this taxon is restricted to Tulare County, California — within, but near the southern range limit of var. *torreyi*. In spite of its variable leaf morphology, the taxon is differentiated because "the wings of each pair of samaras overlap". Although there appears to be a considerable proportion of individuals possessing the peculiar seed-wing character in the type locality, this trait is neither homogeneous in nor unique to that area. For example, overlapping samara wings are not uncommon in var. *diffusum* populations both east and west of the southern Sierra. (See Table 3.1.1. for list of collections with overlapping samara wings.) Collected and herbarium material from Tulare County exhibit a range of leaf morphologies (Figure 5.3.16.): from var. *diffusum*-like to var. *torreyi*-like, to possible intermediates. That this area is situated at the margin of both ranges strongly suggests that plants here probably represent introgressed individuals of these 2 taxa.

Acer glabrum subsp. *siskiyouense* is reported to inhabit territory between that of varieties *torreyi* and *douglasii*, namely, the Siskiyou Mountains. Morphologically, it is



reputed to be intermediate between these 2 taxa, and is described as having rhombic leaf lobes (Murray, 1983). Many *A. glabrum* plants that inhabit this area display rhombic lobes (many do not), and many show leaf shape variation which could be interpreted as var. *douglasii* influence — increased leaf size, for example. Herbarium specimens collected in 6 northern Californian counties also display leaves virtually indistinguishable from the *siskiyouense* "type" (none are any more representative of those local collections, either). Furthermore, analogous variants with rhombic lobes are found throughout the southwestern range of *A. glabrum* (see Figure 5.3.17. for comparison). It is possible, and perhaps likely, that plants in the region of the northern Sierra-southern Cascades represent intermediate, hybrid forms.



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Herbarium Specimens Examined

Acer glabrum var. *glabrum*

Arizona: Apache County: **Mason & Mason 2434**, *Lukachukai Mtns*, UC M280088.

Idaho: Caribou County: **Holmgren 16543**, *Gray's Range*, OGDF. Cassia County: **Wilson 2037**, *10 mi E of Oakley*, (RW?). Emery County: **Lewis 4167**, *mouth of Tie Fork*, OGDF. Fremont County: **Whitehead 1110**, *above Hwy 19*, OGDF; **Wilson 1167**, *Big Falls*, (RW?). Owyhee County: **Wilson 1941**, *Jordan Creek*, (IDSC?).

Utah: Boxelder County: **Holmgren 70**, *Green Canyon, Bear River Range*, UTC 108201; **Maguire & Richards 5195**, *Logan Canyon*, UTC 8982; **McMillan 1504**, *Clear Creek Canyon, Raft River Mtns*, UT 86633; **Preece 880**, *George Creek Canyon, Raft River Mtns*, UT 21554. Cache County: **Shaw 3748**, *Wellsville Mtns*, UTC 186498; **Tillett 358**, *Mt. Magog, White Pine Canyon*, UTC 92948. Carbon County: **Clark & Taylor 2369**, *Price Canyon*, OGDF 169348. Dagget County: **Richens 10**, *Uinta Mtns*, UTC. Garfield County: **Bailey & Bailey 3905**, *Bryce Canyon Nat. Park*, UC 1566826; **Cottam 14116**, *Table Cliff Plateau, Water Canyon Cirque*, UT 86620; **Cottam 14117**, UT 28619; **Everitt 147**, *Henry Mtns*, UT 74687; **Hall (1950)**, *Upper Valley* UT; **Harrison Empey & Larson 7453**, *Bromide, Henry Mtns*, UTC; **Neese & White 3431**, *Henry Mtns*, OGDF. Iron County: **Gierisch**, *10 mi E of Cedar City*, UTC 119157; **Hitchcock, Rethke & vanRaadschooven 462**, *10 mi E of Cedar City*, UT 28678; **Maguire 19430**, *8.5 mi E of Cedar City*, UTC 126536. Kane County: **Cottam (1961)**, *Orderville*, UT 26625. Millard County: **Goodrich 14359**, *S of Foot Peak, nr Oak City*, SSLP 9; **Kass & White 483**, *below Notch Peak, House Range*, UT 96768. Piute County: **Cottam (1961)**, *Deer Creek, Marysville Canyon*, UT 55333. Salt Lake County: **Arnold 845**, *10 mi E of Salt Lake City, Wasatch Mtns*, UT 74885; **Arnold 2907**, *Red Butte Canyon, Wasatch Mtns*, UT 77428; **Cottam, Anderson & Rowland 14930**, *Big Cottonwood Canyon, Wasatch Mtns*, UT; **Garrett 1906**, *Big Cottonwood Canyon, Wasatch Mtns*, UT 26622; **Garrett 3015**, *Big Cottonwood Canyon, Wasatch Mtns*, UT 26621; **Vickery 1507**, *Lamb's Canyon, Wasatch Mtns*, UT; **Vickery 2450**, *Lamb's Canyon, Wasatch Mtns*, UT 51281; **Vickery 2564**, *Mill Creek Canyon, Wasatch Mtns*, UT 61728; **Vickery 2589**, *Lamb's Canyon, Wasatch Mtns*, UT; **Vickery 2641**, *Lamb's Canyon, Wasatch Mtns*, UTC 116429; **Winburn (1965)**, *2 mi SE of Bountiful, Meuller Park*, UT 81643. San Juan County: **Carter 1589**, *6-8 mi W of Monticello, Abajo Mtns*, UTC 54336; **Rydgerg & Garrett 5665**, *Prumley Creek, La Sal Mtns*, NESH 14263. Sevier County: **Warnock (1961)**, *Lower Kimberley, Tushar Mtns*, UT 61116. Tooele County: **Garrett 8813**, *canyon slopes*, UT 26631; **Taye 77**, *S. Willow Canyon, Stansbury Mtns*, UT 90337. Uintah County: **Goodrich 17700**, *Vernal, Uinta Mtns*, SSLP 7. Utah County: **Flowers 336**, *Timpanogos Creek*, UT 10554; **Garrett 3574**, *Mt Timpanogos, Wasatch Mtns*, UT 26626; **Garrett 5665**, *Mt Timpanogos, Wasatch Mtns*, UT 26627; **Moore 91**, *Timpanogos*, UT 10555; **Smith 1922**, *Prov Canyon*, UTC 8976. Weber County: **Call 106**, *Cold Water Canyon*, UT 10547; **Clark 1869**, *Bear Hollow*, UTC 135649.

Wyoming: Albany County: **Porter & Porter 10003**, *Laramie Range*, UC 282308.

Lincoln County: **Shaw 2295**, *Swift Creek Canyon*, UTC 147262; **Shultz 679**, *Wyoming Range*, UTC. Sublette County: **Shultz 361**, *Pine Grove and Riley Ridge*, UTC 155582.

Teton County: **Anderson 121**, *Teton Canyon*, UTC 90981; **Bailey & Bailey 4463a**, *Grand Teton Nat. Park*, UC 1567867; **Shaw 1619**, *Grand Teton Nat. Park*, UTC; **Shaw 1801**,

Grand Teton Nat. Park, UTC 131277; **Shaw 1815**, *Gros Ventre Slide*, UTC 131299; **Shaw 1852**, *Grand Teton Nat. Park*, UTC 131270; **Shaw, McCurdy & Lorimer 1748**, *Grand Teton Nat. Park*, UTC 133429; **Shaw & Shaw 1838**, *Grand Teton Nat. Park*, UTC 131214; **Williams 1344**, *Grand Teton Nat. Park*, UTC 8983.

Acer glabrum var. *diffusum*

Arizona: Coconino County: **Bailey & Bailey 1217**, *Grand Canyon Nat. Park*, UC 1578192; **Buchanan & Hodgson H2269**, *Jacob Lake*, UNLV 24026.

California: Inyo County: **DeDecker 2972**, *Tamarack Canyon*, *Inyo Mtns*, UC 1442688; **Duran 3032**, *Birch Creek*, *White Mtns*, UTC 8972; **Mitchell 2263**, *Wyman Canyon*, *White Mtns*, UC M299864; **Thorne 56113**, *Panamint Mtns*, UT 106301. Mono County: **Duran 2576**, *White Mtn*, UTC 109900. Riverside County: **Hall 2602**, *Tamarack Valley*, *San Jacinto Mtns*, UC 18091. San Bernardino County: **Henrickson 14064**, *Kingston Peak*, *Kingston Mtns*, UC (Chico?) 35722; **Munz 10778**, *Sugarloaf Mtn*, *San Bernardino Mtns*, UC 310235; **Roos 4915**, *Kingston Peak*, *Kingston Mtns*, UC M010290; **Thorne, DeBurhr, Wisura & Prigge 49532**, *Clark Mtns*, UTC 166149.

Nevada: Clark County: **Ackerman 1101**, *Desert Nat. Wildlife Range*, UNLV 12927; **Ackerman 1102**, *Desert Nat. Wildlife Range*, UNLV 13128; **Alexander 575a**, *Charleston Park*, *Charleston Mtns*, UC 625942; **Annable & Peterson 1428**, *Charleston Peak*, *Spring Mtns*, UNLV 19483; **Atwood & Thorne 12638**, *Carpenter Canyon*, UNLV 027030; **Beatley (1971)**, *Clark Canyon*, *Spring Mtns*, UNLV 4888; **Clokey A120**, *Kyle Canyon*, *Charleston Mtns*, OGDF 80891; **Clokey 5531**, *Charleston Park*, *Charleston Mtns*, UTC 24966; **Clokey 8017**, *N. fork of Deer Creek*, *Charleston Mtns*, UC 899326; **Clokey & Bean 7186**, *Harris Springs*, *Charleston Mtns*, UC 899327; **Fisher Jr. 25**, *Deer Creek*, *Spring Mtns*, UNLV 5621; **Fisher Jr. 1146**, *Kyle Canyon*, *Spring Mtns*, UNLV 10463; **Gordon & Leary 4052**, *Red Rock Canyon Rec. Area*, UNLV 032651; **Heller 11001**, *Lee Canyon*, *Charleston Mtns*, UC 175347; **Peterson 1428**, UNLV; **Pinzl 4858**, *Charleston Peak*, *Spring Mtns*, NSMC 6331; **Rivers & Hancock 507**, *Charleston Peak*, *Spring Mtns*, UNLV 6854; **Tiehm & Williams 5454**, *Virgin Mtns*, NESH 63806; **Train 2105**, *Lee Canyon*, *Charleston Mtns*, UNLV 5800; **Williams 160**, *Clark Canyon*, *Charleston Mtns*, UNLV 1239; **Williams 79-171-12**, *Mary Jane Falls*, *Spring Mtns*, NESH 58335; **Williams & Tiehm 79-174-5**, *trail to Cathedral Rock*, *Spring Mtns*, NESH 58334. Elko County: **Cottam 12688**, *Pilot Mtn*, UT 22769; **Heller 9161**, *Clover Mtn*, NESH 9875; **Holmgren 1177**, *Spruce Mtn*, UTC 48773; **Holmgren 1276**, *Spruce Mtn*, UTC 48555; **Holmgren 1801**, *Lamoille Canyon*, UTC 48772; **Lund 98**, NESH 37463; **Tiehm & Williams 9613**, *Pequop Mtns*, UTC 194709. Eureka County: **Pinzl 4319**, *Roberts Mtns*, NSMC 5594; **Tiehm & Williams 8202**, *Fish Creek Range*, UT 189014. Humboldt County: **Heller 10627**, *Humboldt Canyon*, *W Humboldt Mtns*, NESH 13196. Lander County: **Linsdale 395**, *Big Creek*, (?) 84938. Lincoln County: **Tiehm & Williams 7991**, *Schell Creek Range*, NESH 55948; **Train 2553**, *Wilson Mtn*, UNLV 13303. Nye County: **Kurzius 1193**, *Grapevine Mtns*, NSMC 2086G; **Linsdale 272**, *S Fork*, *Mohawk Canyon*, *Toyabee Mtns*, (?) 84939; **McVaugh 6079**, *Troy Canyon*, *Grant Range*, UC 719674; **Pinzl 2438**, *E side of Toiyabe*, NSMC; **Williams 76-43-5**, *Broom Canyon*, UT 153508. Pershing County: **Tiehm 8880**, *W Humboldt Mtns*, NSMC 3184G. White Pine County: **Holmgren 9886**, *Marble Canyon*, *Snake Range*, UTC 192563; **Holmgren & Lewis 15703**, *Snake Range*, UT 110625; **Holmgren & Reveal 1005**, *Swallow*

Canyon, Snake Range, UTC 118936; **Lyman 1157**, *N Snake Range*, UNLV 034042; **Pinzl 3159**, *Egan Range*, NSMC 4158; **Pinzl 4392**, *Kalamazoo Canyon*, Schell Range, NSMC 5515; **Pinzl & Morefield 10052**, *Egan Range*, NSMC 11780; **Robertson & Kittel 64-75**, *Trail Canyon*, *Humboldt Nat. Forest*, UNLV 33795; **Tiehm 9457**, *Pole Canyon*, *Snake Range*, UTC 195867; **Train 1149**, *Baker Creek*, *Snake Range*, UNLV 13361; **Tiehm & Ertter 8977**, *Duck Creek Range*, UT 106069; **Train 1062**, *S Fork*, *Berry Creek*, UNLV 6102.

Utah: Beaver County: **Cottam 8038**, *Wah Wah Mtns*, UT 10561; **Cottam 9054**, *Wah Wah Mtns*, UT 10562; **Goodrich 18570**, *Mtn Home Range*, SSLP 4436; **Goodrich 19316**, *Mtn Home Range*, SSLP 5414; **Holmgren & Beale 342**, *Needle Range*, SSLP 5093. Boxelder County: **Cottam 3106**, *Copper Mtn*, UT 10552. Cache County: **Maguire 15949**, *Spring Hollow*, UTC 21397. Garfield County: **Tuhy 798**, *Upper Henderson Canyon*, UTC 181558; **Weight B-31/90**, *Bryce Canyon*, UT 10558. Juab County: **Maguire & Beecraft 1933**, *Granite Canyon*, UTC 8979; **McMillan 695**, *Granite Creek Canyon*, UT 84057. Millard County: **Lowry, Dickson & Smith 261**, *House Range*, UTC 144508. Tooele County: **Cottam 3202**, *Deep Creek Mtns*, UT 10551; **Detling & Albee**, *Callao*, UT 87325. Utah County: **Cottam 8937**, *Pie Valley*, UT 10545.

Acer glabrum var. *douglasii*

Canada: Alberta: **McCalla 6560**, *Waterton Lakes Nat. Park*, UBC 064847; **Nagy & Blais 316**, *Waterton Lakes Nat. Park*, UBC 133455; **Nagy & Blais 516**, *Waterton Lakes Nat. Park*, UBC 133704; **Ogilvie** (1959), *Banff Nat. Park*, UBC 91885; **Ogilvie** (1960), *Waterton Lakes Nat. Park*, UBC 91886.

British Columbia: **Ashlee** (1955), *Saltspring Island*, UBC 765693; **Ashlee** (1956), *Mayne Island*, UBC 765694; **Ashlee** (1958), *Saltspring Island*, UBC 765695; **Beamish 7727**, *Manning*, UBC 78601; **Beamish 7762**, *Manning*, UBC 78553; **Beamish 8099**, *Summerland*, UBC 76270; **Beamish & Franko 13**, *nr Princeton*, UBC 177777; **Beamish, Luitjens & Krause** (1968), *Penticton*, UBC 136161; **Beamish, Luitjens, Campbell & Carey 750144**, *Slocan Lake*, UBC 164265; **Beamish & Vrugtman 60062**, *Oliver*, UBC 84355; **Beamish & Vrugtman 60295**, *Hedley*, UBC 84356; **Beamish & Vrugtman 60401**, *Greenwood*, UBC 84358; **Beamish, Vrugtman & McK.** (1961), *Allison Lake*, UBC 136158; **Beil** (1967), *Williams Lake*, UBC 148678; **Beil** (1978), *Williston Lake*, UBC 161078; **Beirne 2-049**, *Hat Creek*, UBC 159959; **Bell** (1964), *Stevens Creek*, UBC 109314; **Bell & Davidson 15**, *Fernie*, UBC 67087; **Bell & Davidson 756**, *Mt Flathead*, UBC 67086; **Brink** (1947), *Michel*, UBC 113318; **Brink 50-44**, *Radium*, UBC 72214; **Brink** (1971), *Prince George*, UBC 173496; **Buckland Ac1**, *Youbou*, UBC 5734; **Calder & MacKay 29245**, *Oyster River*, *Vancouver Island*, UBC 119628; **Calder, Parmalee & Taylor 16326**, *Sydney*, UBC 77936; **Calder, Savile & Ferguson 13584**, *Fort St James*, UBC 62224; **Chuang 1144**, *Skagit Camp*, *Manning Park*, UBC 149871; **Davidson** (1912), *Stoney Creek*, *Pemberton*, UBC 5723; **Davidson** (1913), *Spences Bridge*, UBC 5714; **Davidson** (1914), *Spences Bridge*, UBC 5726; **Davidson** (1915), *Three Sisters Valley*, UBC 5715; **Davidson** (1915), *Three Sisters Valley*, UBC 68553; **Dickens 130**, *Tzoonie River*, UBC 83122; **Eastham** (1937), *Nelson*, UBC 5709; **Eastham** (1938), *Nelson*, UBC 5708; **Eastham** (1944), *Smithers*, UBC 5720; **Eastham** (1945), *Fort St James*, UBC 5721; **Eastham** (1947), *Lytton*, UBC 5711; **Eastham** (1947), *Fairmont Hot Springs*, UBC 5733; **Finlayson** (1898), *Sicamous*, UBC 43558; **Fodor**

(1961), *Hope-Princeton*, UBC 92496; **Fodor 422**, *Kimberly*, UBC 116133; **Fodor 987**, *Sorrento*, UBC 165226; **Foster 105**, *Maroon Cr. Valley*, UBC 166246; **Gagnon, Spiers & Palmer 81-62-3**, *W Central Vancouver Island*, UBC 197672; **Gagnon, Spiers & Palmer 81-99-8**, *W Central Vancouver Island*, UBC 197694; **Gorman 1458**, *Iskit River*, UBC V176905; **Gorman 1482**, *Iskit River*, UBC V176923; **Gorman 3210**, *Iskit River*, UBC V177383; **Gornall 0231**, *Lillooet*, UBC 165840; **Graham 440**, *Moberley*, UBC 95595; **Griffith** (1968), *Penrose Island*, UBC 184701; **Gruchy** (1940), *Cayoosh Creek, Lillooet*, UBC 137026; **Harrington G622**, *Thetis Island*, UBC 71929; **Henry** (1898), *Vancouver*, UBC 5724; **Holm & Vrugtman 29**, *Bowen Island*, UBC 78930; **Holman** (1916), *Kootenay Lake*, UBC 5725; **Jones** (1979), *plot 24, Power River, Vancouver Island*, UBC V167769; **Kojima** (1968), *Strathcona Park*, UBC 151498; **Krajina 1393**, *Lytton*, UBC 88673; **Krajina** (1952), *Falkland*, UBC 79497; **Krajina 1185**, *Lytton*, UBC 89470; **Krajina** (1952), *Revelstoke*, UBC 103755; **Krajina** (1963), *Mabel Lake*, UBC 101959; **Krajina & Pojar** (1974), *McKenzie*, UBC 145512; **Krajina, Pojar & Parsons** (1974), *Tyee Lake*, UBC 148410; **Krajina, Pojar & Parsons** (1974), *Quesnel*, UBC 148489; **Krajina, Pojar & Parsons** (1974), *McGregor*, UBC 152366; **Krajina, Pojar & Parsons** (1974), *Telkwa*, UBC 152663; **Krajina, Pojar & Parsons** (1974), *Purden Lake*, UBC 152707; **Krajina, Pojar & Parsons** (1974), *McKenzie*, UBC 163437; **Krajina, Spilsbury & Szczawinski 4508**, *1st Nanaimo Lake*, UBC 46723; **Krajina, Spilsbury & Szczawinski 4583**, *Qualicum Beach*, UBC 46722; **Krajina, Spilsbury & Szczawinski 5280**, *Nanaimo River valley*, UBC 46721; **Kruckeberg 28**, *Pinchi Mine*, UBC 172320; **Landells** (1914), *Golden*, UBC 5727; **Lundborg 85**, *Jct. Chilcoten and Fraser Rivers*, UBC 179554; **Marchant** (1977), *Williams Lake*, UBC 161854; **McCalla 4568**, *Field*, UBC 65660; **McCalla 6835**, *Fernie*, UBC 65642; **McCalla 8086**, *Nelson*, UBC 61449; **McCalla 9236**, *Field*, UBC 61317; **Ocsko** (1957), *Kimberley*, UBC 137592; **Ocsko & Ravay** (1957), *Powell River*, UBC 137593; **Oseko 8**, *Kimberley*, UBC V183189; **Perry** (1918), *Lytton*, UBC 5707; **Pillsbury 126**, *Bulkley Valley*, UBC 52197; **Pillsbury 199**, *Kispiox River*, UBC 58031; **Pillsbury 201**, *Skeena River*, UBC 58033; **Pillsbury 202**, *Hazelton*, UBC 58032; **Pillsbury 217**, *Hazelton*, UBC 52196; **Pinder-Moss & Pojar 675**, *Cayoosh Creek, Lillooet*, UBC 156902; **Pojar** (1974), *Brew Mtn, Daisy Lake*, UBC 144631; **Pojar & Pinder-Moss 72**, *Woss Lake*, UBC 141071; **Rattenbury** (1946), *Nicomien River*, UBC 82845; **Ravai & Ocsko** (1957), *Kimberley*, UBC 148013; **Revel** (1967), *McLeod Lake*, UBC 133909; **Revel** (1967), *McLeod Lake*, UBC 133910; **Revel** (1968), *Tacheeda Lake*, UBC 133911; **Rhodes 7**, *Stamp River, Alberni*, UBC 45080; **Roche** (1966), *Cranbrook*, UBC 136159; **Roche** (1966), *Nelson*, UBC 136160; **Rogers** (1951), *Oliver*, UBC 95310; **Rose** (1976), *Fairmont Hot Springs*, UBC 190037; **Sanderson 37**, *Smithers*, UBC 5716; **Sanderson** (1950), *Slocan Valley*, UBC 5717; **Schmidt 18b**, *Terrace*, UBC 71065; **Schmidt 23**, *Terrace*, UBC 71093; **Schofield & McIntosh** (1979), *Peachland*, UBC V165108; **Sharp 3**, *Stein Valley*, UBC V180149; **Straley 4308**, *Mayne Island*, UBC V193169; **Straley 7915**, *North Fork Rd, Grand Forks*, UBC 208770; **Straley 7916**, *North Fork Rd, Grand Forks*, UBC 208769; **Szczawinski** (1964), *Golden*, UBC 132998; **Taylor** (1933), *Quesnel*, UBC 5706; **Taylor** (1933), *Quesnel*, UBC 5719; **Taylor 6190**, *Gang Ranch*, UBC 183784; **Taylor & Ferguson 2060**, *Flathead*, UBC 77889; **Taylor & Lewis 3**, *Pavilion Lake*, UBC 38060; **Taylor & Lewis 141**, *Shalalth*, UBC 38061; **Taylor & Lewis 579**, *Hazelton*, UBC 38059; **Taylor, Krajina & Tusko 4**, *Seton Lake*, UBC 83402; **Taylor, Krajina & Tusko 6**, *Pavilion Lake*, UBC 83385; **Taylor & Szczawinski 96**, *Kyuquot*,

Vancouver Island, UBC 74452; **Taylor & Szczawinski 224**, *Kyuquot, Vancouver Island*, UBC 74453; **Taylor & Szczawinski 556**, *Gerrard*, UBC 94781; **Taylor, Szczawinski & Bell 1515**, *Haines Rd, Mile 45*, UBC 56357; **Teit** (1912), *Thomson Valley*, UBC 5730; **Thacker** (1914), *Dryas Island (Hope)*, UBC 43547; **Thacker** (1914), *Dryas Island (Hope)*, UBC 43548; **Tisdale** (1938), *Tranquille Range*, UBC 5731; **Toner** (1944), *Jct Fraser and Chilcoten Rivers*, UBC 5718; **Turner 462**, *Whistler Mtn*, UBC 140019; **Vrugtman 1567**, *Lytton*, UBC 103887; **Vrugtman 610201**, *Oliver*, UBC 88918; **Vrugtman 610316**, *Oliver*, UBC 88919; **Vrugtman & Beamish 625**, *Manning*, UBC 59928; **Wilkeem & Gale** (1978), *Kaleden*, UBC V169046; **Wilson 13**, *Armstrong*, UBC 5713; **Wilson 31**, *Armstrong*, UBC 5712; **Wilson 890**, *Armstrong*, UBC 43556; **Wright** (1977), *Vernon*, UBC V168432.

United States: Alaska: **Taylor 6560A**, *Admiralty Island*, UBC 163919.

Idaho: **Krajina** (1963), *Lookout Pass*, UBC 102590. Bannock County: **Wilson** (1939), *Caribou Nat. Forest*, (U of Idaho?). Boundary County: **Wilson 706**, *6 mi W of Bonners Ferry*, (RW?); **Wilson 1879**, *Fall Creek*, (RW?). Clearwater County: **Wilson 1839**, *Orogrande Creek*, (RW?). Idaho County: **Wilson 2232**, *Crooked Fork Creek*, OGDF. Owyhee County: **Clarkson 230**, UBC 91515. Payette County: **Sparhawk 188**, *Warm Springs Creek*, OGDF. Shoshone County: **Wilson 590**, *1.5 mi W of Mullan*, (RW?); **Wilson 1850**, *Bullion Creek*, (RW?).

Montana: Flathead County: **Wilson** (1948), UT.

Washington: Chelan County: **Dress 4303**, UBC 125582.

Acer glabrum var. *neomexicanum*

New Mexico: Catron County: **Gillett & Moulds 12822**, UBC 111564. Socorro County: **Eggleston 16821**, UBC 5722.

Acer glabrum var. *torreyi*

California: Del Norte County: **Straley 7355**, UBC V19140. El Dorado County: **Robbins 2032**, *above Island Lake*, UTC 76211; **Kennedy 222**, *Spring Meadows, Eldorado Nat. Forest*, UC (Davis?) 17. Placer County: **Billings 2132**, *1-2 mi S of The Cedars*, UNLV. Sierra County: **Straley & Taylor 1873**, UBC 162632. Siskiyou County: **Jepson 2837**, *Marble Mtn*, JEPS 42741; **Bacigalupi 6801**, *Castle Lake*, JEPS 24792. Tulare County: **Bailey & Bailey 2619a**, *Paradise Valley*, UC 1564857; **Bailey & Bailey 2800**, *Bubb's Creek*, UC 1564858; **Ferris & Lorraine 10663**, *.5 mi from Mineral King P.O.*, UTC 69894; **Henrickson 5606**, *1 mi N of Mineral King*, UNLV 6062; **Mallory 336**, *Maggie Mtn*, UC (Davis?) 57277; **Rice 128**, *2.5 mi SE of Mineral King*, UC (Davis?) 40913; **Rice 308**, *Crystal Creek*, UC (Davis?) 41045.

Nevada: Washoe County: **Pinzl 3798**, *Carson Range*, NSMC 4160.

Acer glabrum var. *glabrum* - var. *diffusum* Intermediates

Arizona: Coconino County: **Risk 2**, *Grand Canyon Nat. Park*, UNLV 4330.

Nevada: Elko County: **Holmgren 1897**, *Jarbridge*, UTC 48554; **Lewis & Walters 4545**, *Jarbridge Wilderness*, UTC 151436; **Pinzl 3690**, *Jarbridge River*, NSMC 4159.

Utah: Cache County: **Maguire 3544**, *Dry Canyon, 4 mi E of Logan*, UTC 8980; **Maguire 13731**, *Dry Canyon, 4 mi E of Logan*, UTC 120167. Iron County: **Hitchcock, Rethke & vanRaadshooven 4622**, *nr Cedar Breaks*, UTC 125382.

Acer glabrum var. *glabrum* - var. *neomexicanum* Intermediates

Utah: Emery County: **Jorgensen 33**, *Huntington Canyon*, UT 21709. Piute County: **Cottam** (1962), *Lower Kimberley, Tushar Mtns*, UT 85887. San Juan County: **Maguire & Redd 1960**, *South Peak, Abajo Mtns*, UT.

Acer glabrum var. *glabrum* - var. *douglasii* Intermediates

Idaho: Bannock County: **Wilson 2088**, *6 mi NE of Inkom*, (RW?). Latah County: **Wilson 2171**, *Moscow Mtns*, (Idaho State College?). Lehmi County: **Wilson 846**, *Salmon River*, (RW?). Washington County: **Lewis 2228**, *West Pine Creek*, OGDF.

Acer glabrum var. *diffusum* - var. *neomexicanum* Intermediates

Utah: Millard County: **Goodrich 16843**, *6 mi NW of Scipio*, SSLP 239448.

Acer glabrum var. *diffusum* - var. *torreyi* Intermediates

California: Placer County: **Brainerd & Baird 189**, *Bear Mtn (?)*, JEPS 59454. Tulare County: **Smith 831**, *Baker Point, Baker Range*, JEPS 48551; **Smith 979**, *Tobias Gorge, Baker Range*, JEPS 39585.

Nevada: Washoe County: **Herlan & Porter** (1976), *Sawmill Canyon*, NSMC 2498.

Acer circinatum (labelled *Acer glabrum* \times *Acer circinatum* ?)

British Columbia: **R. L. Taylor 5228 & D. A. Tarrant**, *1.7 mi S of Hell's Gate tunnel on Hwy 1*, UBC 180424.

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - IDAHO

ACERACEAE

Acer glabrum var. *douglasii* (Hook.) Dippel

Tree to 10m, multi-stemmed. Bark grey. Twigs glabrous, reddish. Leaves green above, lighter below; 3-parted on vigorous basal shoots; yellow autumn colour. Seed wings straight, broad, held at an acute angle.

Elevation 1000m. Off Interstate 90, opposite Lake Coeur d'Alene, Kootenai County. Top of south-facing slope, road-edge. Shaded site. Soil gravelly with thin humus layer. With *Pseudotsuga menziesii*, *Pinus ponderosa*, *Amelanchier alnifolia*, *Acer platanoides*.

Coll.: D. Justice N^o 001 & K. Justice

Date: 19 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - WASHINGTON

ACERACEAE

Acer glabrum var. *douglasii* (Hook.) Dippel

Tree to 6m, multi-stemmed, branches recurved. Bark grey-brown. Twigs glabrous, reddish-brown, green in shade and on vigorous upright shoots. Leaves green above, lighter below; 3-parted to -lobed on vigorous upright shoots; yellow autumn colour.

Elevation <100m. Off Highway 20, pull-off opposite Pass Lake, Deception Pass, Skagit County. Steep, north-facing slope, heavily shaded. Soil thin, humusy, moist, over granite bedrock. With *Abies grandis*, *Tsuga heterophylla*, *Alnus rubra*, *Gaultheria shallon*, *Polystichum munitum*.

Coll.: D. Justice N^o 004 & K. Justice

Date: 03 Oct 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - COLORADO

ACERACEAE

Acer glabrum var. *glabrum* Torrey

Shrub to 4m. Bark grey-brown. Twigs glabrous, dark brown. Leaves green above, lighter below; deeply 3-lobed on vigorous basal shoots; yellow autumn colour. Seed wings straight, broad, held at an acute angle.

Elevation 1900m. Off Highway 119, parking lot opposite Boulder Canyon Park,

Boulder, Boulder County. Steep, north-facing rocky slope. Soil gravelly with thin humus layer. With *Acer negundo*, *Pinus ponderosa* var. *scopulorum*, *Amelanchier alnifolia*, *Mahonia repens*, *Opuntia phaeacantha*.

Coll.: D. Justice N^o 005 & K. Justice

Date: 21 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - COLORADO

ACERACEAE

Acer glabrum var. *glabrum* Torrey

Shrub to 4m. Bark grey-brown. Twigs glabrous, dark brown. Leaves green above, lighter below; deeply 3-lobed to -parted on extension growth; yellow autumn colour. Seed wings straight, very small, held at an acute angle.

Elevation 2600m. Adjacent to Highway 285, Shawnee (between Grant and Bailey), Park County. Steep, north-facing rocky slope. Soil gravelly with thin humus layer. With *Populus tremuloides*, *Pinus contorta* var. *murrayana*, *Pseudotsuga menziesii*, *Ribes* spp., *Arctostaphylos uva-ursi*.

Coll.: D. Justice N^o 006 & K. Justice

Date: 22 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - ARIZONA

ACERACEAE

Acer glabrum var. *glabrum* Torrey

Shrub to 6m. Bark grey-brown. Twigs glabrous, dark brown. Leaves green above, lighter below; deeply 3-lobed to -parted on extension growth; yellow to orange autumn colour. Seed wings curved, broad, held at an acute angle.

Elevation 3000m. Near summit of Bill Williams Mountain (near Flagstaff), Coconino County. Steep, northwest-facing rocky slope. Soil gravelly with thin humus layer. With *Populus tremuloides*, *Pseudotsuga menziesii*, *Ribes* spp., *Vaccinium* sp.

Coll.: D. Justice N^o 008 & K. Justice

Date: 24 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - NEW MEXICO

ACERACEAE

Acer glabrum var. *neomexicanum* (Greene) Kearney & Peebles

Tree to 8m, multi-stemmed. Bark grey-brown. Twigs glabrous, brown. Leaves green above, lighter below; 3-parted on extension growth; yellow to orange autumn colour. Seed wings straight, broad, held at an acute angle.

Elevation 2800m. Outside Hyde Memorial State Park, above Santa Fe, Santa Fe County. Riparian. Steep, southwest-facing forested slope. Soil gravelly with thin humus layer. With *Populus tremuloides*, *Pseudotsuga menziesii* var. *glauca*, *Pinus ponderosa*, *Abies concolor*, *Rubus parviflorus*.

Coll.: D. Justice N^o 010 & K. Justice

Date: 23 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - NEW MEXICO

ACERACEAE

Acer glabrum var. *neomexicanum* (Greene) Kearney & Peebles

Shrub to 5m. Bark grey-brown. Twigs glabrous, dark brown. Leaves green above, lighter below; occasionally 3-parted on extension growth; yellow to orange autumn colour. Seed wings straight, narrow to broad, held at an acute angle.

Elevation 2700m. Sandia Peak, above Placitas, Bernalillo County. Riparian. Northeast-facing forested slope. Soil gravelly with thick humus layer. With *Acer negundo*, *Robinia neomexicanum*, *Pinus ponderosa*, *Abies concolor*.

Coll.: D. Justice N^o 013 & K. Justice

Date: 23 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - UTAH

ACERACEAE

Acer glabrum var. *neomexicanum* (Greene) Kearney & Peebles

Shrub to 4m. Bark grey-brown. Twigs glabrous, reddish-brown. Leaves green above, lighter below; deeply lobed on extension growth; yellow autumn colour. Seed wings curved, narrow to broad, held at an acute angle.

Elevation 2400m. Northwest facing stream banks along Hwy 14, 16 km east of Cedar

City, Iron Co. Soil gravelly with thin humus layer. With *Pseudotsuga menziesii*, *Picea pungens*, *Cornus stolonifera*, *Populus tremuloides*, *Abies concolor*.

Coll.: D. Justice N° 017 & K. Justice

Date: 26 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - NEVADA

ACERACEAE

Acer glabrum var. *torreyi* (Greene) Smiley

Shrub to 8m. Bark grey-brown. Twigs glabrous, brown. Leaves green above, lighter below; yellow autumn colour. Seed wings straight, narrow to broad, held at an acute angle.

Elevation 2400m. Off Hwy 50, northeast slope, above Lake Tahoe, Douglas County. Shaded site. Soil sandy/gravelly, dry. With *Abies magnifica*, *Pinus jeffreyi*, *Amelanchier alnifolia*, *Rubus parviflorus*.

Coll.: D. Justice N° 020 & K. Justice

Date: 27 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - CALIFORNIA

ACERACEAE

Acer glabrum var. *torreyi* (Greene) Smiley

Shrub to 3m. Bark grey. Twigs glabrous, reddish. Leaves green above, lighter below; yellow autumn colour. Seed wings straight to curved, narrow to broad, held at an acute angle.

Elevation 1900m. Off Hwy 89, adjacent to Bluff Falls (Between Mineral and Lassen gate), Tehama County. Gentle, east-facing slope near stream margin. Shaded site. Soil gravelly with thin humus layer. With *Abies magnifica*, *A. concolor*, *Pinus monticola*, *P. contorta* var. *murrayana*, *Amelanchier alnifolia*, *Alnus* sp., *Dicentra uniflora*.

Coll.: D. Justice N° 023 & K. Justice

Date: 30 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - OREGON

ACERACEAE

Acer glabrum var. *torreyi* (Greene) Smiley

Shrub to 4m. Bark grey-brown. Twigs glabrous, red. Leaves green above, lighter below; yellow autumn colour. Seed wings straight, broad, held at an acute angle.

Elevation 1800m. Below ski hill; steep, northeast slope of Mount Ashland, Jackson County. Soil rocky/gravelly with thin humus layer. With *Abies magnifica*, *Alnus rubra*, *Ribes* spp., *Arctostaphylos* sp., *Asarum caudatum*, *Actaea rubra*.

Coll.: D. Justice N° 025 & K. Justice

Date: 01 Oct 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - CALIFORNIA

ACERACEAE

Acer glabrum var. *torreyi* Keller

Shrub to 6m. Bark grey-brown. Twigs glabrous, brown. Leaves green above, lighter below; yellow autumn colour. Seed wings strongly curved, broad, overlapping or nearly so.

Elevation 2000m. Off road to Mineral King, Tulare County. Steep, northwest-facing rocky slope with high forest canopy. Soil rocky, granitic sand, thin humus. With *Abies magnifica*, *Pinus contorta* var. *murrayana*, *P. jeffreyi*, *Corylus californica*, *Arctostaphylos* sp., *Cornus stolonifera*.

Coll.: D. Justice N° 028 & K. Justice

Date: 29 Sept 1993

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of the UNITED STATES - OREGON

ACERACEAE

Acer glabrum var. *douglasii* (Hook.) Dippel

Tree to 10m, multi-stemmed. Bark grey. Twigs glabrous, reddish. Leaves green above, lighter below. Seed wings straight, broad, held at an acute angle, reddish.

Elevation 1000m. Off Highway 26, near mile 74, Mt. Hood National Forest, Wasco County. On gentle NE facing slope, at road-edge (north side) by stream. Moist, shaded site (high coniferous canopy). Soil gravelly-sand with thin humus layer. With *Abies grandis*, *Pseudotsuga menziesii*, *Pinus ponderosa*, *Populus trichocarpa*, *Acer circinatum*, *Thuja plicata*, *Sambucus cerulea*, *Ceanothus velutinus*.

Coll.: D. Justice Nº 030

Date: 22 June 1994

UNIVERSITY OF BRITISH COLUMBIA HERBARIUM (UBC)

Plants of CANADA - BRITISH COLUMBIA

ACERACEAE

Acer glabrum var. *douglasii* (Hook.) Dippel

Tree to 8m, multi-stemmed. Bark grey. Twigs glabrous, reddish. Leaves green above, lighter below. Seed wings straight, broad, held at an acute angle.

Elevation 10m. Top of escarpment, off Bill Murray Way, opposite VIA Rail Station, Prince Rupert. Moist site. Soil sandy with thick humus layer, over unconsolidated glacial till. With *Sambucus racemosa*, *Rubus spectabilis*, *Alnus rubra*, *Polystichum munitum*.

Coll.: D. Justice Nº 031

Date: August 1994

Morphometrics Data Set: Taxon Statistics

var. *diffusum*

Number of cases: 176

	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ
min	3.000	5.000	4.000	2.000	0.000	4.000	0.000	9.000	2.000	0.000
max	5.000	25.000	16.000	13.000	23.000	21.000	19.000	36.000	7.000	2.000
mean	3.557	10.580	7.784	4.273	7.352	9.040	7.841	14.830	4.540	0.739
variance	0.808	7.536	3.565	2.028	10.012	6.027	11.392	11.079	1.164	0.286
std dev'n	0.899	2.745	1.888	1.424	3.164	2.455	3.375	3.329	1.079	0.534

var. *douglasii*

Number of cases: 335

	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ
min	3.000	22.000	7.000	7.000	0.000	12.000	0.000	20.000	5.000	1.000
max	7.000	101.000	55.000	35.000	65.000	73.000	74.000	118.000	38.000	6.000
mean	4.075	51.060	23.925	17.388	32.385	34.036	35.636	57.952	15.424	2.304
variance	1.189	244.086	78.674	32.675	130.267	130.657	208.035	400.543	22.251	1.087
std dev'n	1.090	15.623	8.870	5.716	11.413	11.431	14.423	20.014	4.717	1.042

var. *glabrum*

Number of cases: 268

	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ
min	3.000	11.000	5.000	3.000	0.000	6.000	0.000	11.000	3.000	0.000
max	7.000	46.000	27.000	24.000	31.000	37.000	33.000	54.000	19.000	5.000
mean	4.948	23.433	13.284	8.604	14.299	18.388	15.683	29.799	7.631	1.869
variance	0.312	33.512	17.395	6.937	31.881	20.703	43.244	59.907	5.852	0.541
std dev'n	0.558	5.789	4.171	2.634	5.646	4.550	6.576	7.740	2.419	0.735

var. *neomexicanum*

Number of cases: 337

	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ
min	3.000	12.000	2.000	3.000	0.000	8.000	0.000	10.000	3.000	1.000
max	5.000	55.000	25.000	24.000	26.000	42.000	23.000	71.000	22.000	5.000
mean	3.623	30.855	13.359	11.546	5.555	22.163	5.588	34.858	10.377	2.193
variance	0.861	85.303	16.302	12.909	42.057	42.804	52.035	109.390	14.579	0.775
std dev'n	0.928	9.236	4.038	3.593	0.735	6.542	7.214	10.459	3.817	0.880

var. *torreyi*

Number of cases: 420

	LOB	TTL	BTL	TL1	TL2	SEC	SS	ML	TTH	TSZ
min	3.000	7.000	6.000	3.000	4.000	7.000	0.000	12.000	3.000	0.000
max	5.000	56.000	28.000	24.000	31.000	41.000	38.000	71.000	21.000	3.000
mean	4.052	24.095	13.526	9.224	15.548	19.102	16.414	30.429	8.900	1.281
variance	1.000	62.998	15.438	11.802	18.773	34.846	24.501	82.379	8.548	0.365
std dev'n	1.000	7.937	3.929	3.435	4.333	5.903	4.950	9.076	2.924	0.604