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THE UNIVERSITY OF OTTAWA

A BIOSYSTEMATIC STUDY OF *POLYGONUM ACHOREUM* AND *P. ERECTUM*
(SECTION *POLYGONUM*).

by

Deborah Susan Katz

A THESIS

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Deborah S. Katz, Ottawa, Canada, 1988.

Dedication

To my sister Lauren.

Acknowledgments

I would first like to thank my supervisor Dr. John McNeill for suggesting this project and for many enlightening discussions, without which my labmate Laurie Consaul and I would not have had anything to discuss over the last three years. Motivated by John's tremendous energy and enthusiasm, Laurie and I learned the importance of instant soup and late-night Chinese restaurants. Not without mention is John's famous car (may it rest in peace) which has transported myself and 'the lab gang' to meetings, field collecting trips, birthday and Christmas lunches, and safely home in blizzards!

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Abstract

Although most authors in this century have considered *Polygonum achoreum* Blake and *P. erectum* L. as separate species, Mertens and Raven (1965) reduced *P. achoreum* to synonymy under *P. erectum*, whereas Löve and Löve (1982) have treated *P. achoreum* as a subspecies of *P. erectum*. Results from cluster, principal component and canonical variate analyses, performed on vegetative, fruiting perianth and achene characters, reveal that the taxa are distinct. Each taxon possesses a unique foliar flavonoid profile which does not vary across their geographic ranges. The taxa have different ecological requirements, and phenological differences were evident in the field and greenhouse. The basic chromosome number for the section is $x = 10$, with *P. achoreum* $2n = 40$ and $2n = 60$, and *P. erectum* $2n = 40$. The degree of morphological, flavonoid and phenological differentiation suggests that the taxa should be distinguished at specific rank.

Polygonum achoreum, relatively unknown prior to its late description in 1917, is presently found from the Northwest Territories, south to Colorado, and from British Columbia in the west to Newfoundland in the east. Well established during the nineteenth and early part of this century, the range of *P. erectum* has since receded and it is now rare in southern Ontario, Illinois and Missouri, and infrequent in several southeastern states in the United States. Greater salt tolerance by *P. achoreum* and its ability to withstand the effects of urbanization, appear both to be factors contributing to the increase in the range of *P. achoreum* and to the simultaneous decline of *P. erectum* over this century.

A taxonomic revision of *P. achoreum* and *P. erectum* including a key, descriptions, synonymies, distribution maps, and listings of representative specimens is also presented.

Résumé

Quoique la plupart des auteurs de ce siècle avaient considéré *Polygonum achoreum* Blake et *P. erectum* L. comme espèces séparées, Mertens et Raven (1965) ont réduit *P. achoreum* à comme synonyme de *P. erectum* et Löve et Löve (1982) ont traité *P. achoreum* comme sous-espèce de *P. erectum*. Les résultats obtenus par les analyses de groupement, composantes principales et canoniques faites sur des caractères végétatifs, le perianth en fruit et l'achene, démontrent que les taxons sont distincts. Chaque taxon a un profil de flavonoïdes foliaires unique qui ne varie pas avec leur distribution géographique. Les taxons ont des besoins écologiques différents et les différences phénologiques sont évidentes dans le champ et la serre. Le nombre chromosomique de base pour cette section est $x=10$, pour *P. achoreum* $2n=40$ et $2n=60$, et pour *P. erectum* $2n=40$. Les différences morphologiques, flavonoïques, et phénologiques suggèrent qu'il s'agit d'espèces distinctes.

Polygonum achoreum, très peu connu avant sa description tardive en 1917, est présentement retrouvé des Territoires du Nord-Ouest au sud du Colorado, de la Colombie-Britannique dans l'ouest à Terre Neuve dans l'est. Très bien établie pendant le dix-neuvième et le début de vingtième siècle, la distribution géographique de *P. erectum* a diminué. *Polygonum erectum* est présentement rare dans le sud de l'Ontario, l'Illinois et le Missouri, et infrequent dans quelques états du sud-est des États Unis. Sa plus haute tolérance pour les sels et son abilité de ne pas être très affecté par les effets d'urbanisation paraissent être les facteurs contribuant à l'expansion de *P. achoreum* et le déclin simultané de *P. erectum* pendant ce siècle.

Une révision taxonomique de *P. achoreum* et *P. erectum* est présentée. Cette révision inclut une clé des descriptions, des synonymes, des cartes de distribution et des listes spécimens.

I. INTRODUCTION

Polygonum achoreum Blake and *P. erectum* L. are members of the genus *Polygonum* L. in Section *Polygonum* (often called Section *Aviculare* L. in earlier literature). These annual herbs occur in naturally disturbed and ruderal habitats in North America. Plants of *P. erectum* are restricted to temperate regions, whereas plants of *P. achoreum* have a much larger range, occupying temperate, boreal and subarctic regions.

Blake (1917) considered *P. achoreum* to be closely related to *P. erectum* and distinguished the two taxa by characters of the leaves, fruiting perianth and ochreae. Most authors in this century have considered *P. erectum* and *P. achoreum* to be separate species. However, in a study based solely upon herbarium specimens, Mertens and Raven (1965) reduced *P. achoreum* to synonymy under *P. erectum* because they could not find any morphological differences between the species. Furthermore, Löve and Löve (1982) have treated *P. achoreum* as a subspecies of *P. erectum*, but did not provide any justification for their treatment. Although *P. erectum* has most often been confused with *P. achoreum*, recent evidence (Wolf and McNeill 1986, 1987) suggests that these taxa may be distinct at the specific level.

A. Taxonomic History

Polygonum erectum was first collected in Philadelphia, Pennsylvania by Kalm in 1748 (Benson 1966, Forster 1972). Linneaus (1753) based his description of *P. erectum* on material grown from seed sent to him by Kalm. This taxon has always been considered endemic to North America. However, names based on *P. aviculare* L. and its varieties, originally applied to Eurasian plants, have been misapplied to North American plants of *P. erectum*, resulting in nomenclatural confusion.

Polygonum achoreum was first described from Burlington, Vermont by Blake in 1917. Although Blake regarded *P. achoreum* as "indigenous to the United States", he noted that it had not been found in a clearly native condition, and hence gave it the epithet *achoreum*, meaning without a native land. Several taxonomists (Fernald 1950, Marie-Victorin 1964, Gleason and Cronquist 1963) agree that *P. achoreum* is probably indigenous to North America, while others (Gleason 1952, Kaul *et al.* 1986) consider *P. achoreum* to be introduced and of unknown origin.

B. Morphology

Members of Section *Polygonum* have flowers that are scentless, and inconspicuous in size and colour, and position on the plant, and show no adaptation to out-breeding. The flowers are almost entirely self-pollinating and often cleistogamous, with hybridization extremely rare (Styles 1962). Consequently, the within population morphological variation exhibited by the members of Section *Polygonum* has been attributed to varying environmental factors, such as soil nutrients, moisture, and density. These factors have been reported to affect vegetative morphology and habit to the degree that one individual could be identified as belonging to different taxa at various stages of its developmental history (Robinson 1902, Brenckle 1941). One example of this is the relationship between achene morphology and plant maturity. Late in the growing season many members of Section *Polygonum* produce achenes which are atypical from those produced regularly at the time of main fruit set. These achenes are more elongated, smoother, olivaceous, lanceolate, possess a thinner seed coat and are more exserted from the perianth than regular achenes (Brenckle 1946, Gleason 1952, Styles 1962, Mertens and Raven 1965). Needless to say, this variation in morphology, whether due to environmental factors or plant development, has resulted in a proliferation of names in the section (Wolf and McNeill 1986).

Savage and Mertens (1968) note that *P. buxiforme* Small, also a member of Section *Polygonum*, is often misidentified as *P. erectum*, or as *P. aviculare*. Hitchcock *et al.* (1964) describe *P. achoreum* as very similar to *P. aviculare* and often misidentified as *P. buxiforme*. Mitchell and Dean (1978) explain that *P. achoreum* is so variable in habit that it is often misidentified as *P. buxiforme* when prostrate, and *P. erectum* when erect. Due to this apparent confusion, representative specimens of *P. buxiforme* will be included in this study.

To date, no quantitative morphological investigation of *Polygonum* has considered *P. achoreum* and *P. erectum*. A morphometric study of these two taxa, incorporating data from natural field populations and representative herbarium specimens from throughout their ranges, is presented in an effort to clarify their taxonomic relationships, and to document variation, in so far as it exists, within each taxon.

C. Cytology

The basic chromosome number for Section *Polygonum* is $x = 10$ (Löve and Löve 1956, Wolf and McNeill 1987). Löve and Löve (1956) have reported that the eastern North American members of this section consist of diploid, tetraploid, hexaploid, and octoploid individuals. However, other workers doubt the existence of diploids and octoploids having determined only tetraploid and hexaploid individuals from the section in North America (Mertens and Raven 1965, Savage and Mertens 1968, Moore *et al.* 1970, Wolf and McNeill 1987).

Löve and Löve (1956) showed that the 21 taxa of *Polygonum* examined (including *P. erectum* and *P. achoreum*), all possessed an almost median centromere and could not be distinguished morphologically. Karyological studies, therefore, would not be useful to delimit taxa within this section.

Previously reported chromosome numbers for *P. achoreum* and *P. buxiforme* are presented in Table 1. An undocumented count of $2n = 20$ for *P. buxiforme* reported by Löve and Löve (1956) appears questionable and is not included. Å. Löve (pers. comm. 1986) has stated that the count of $2n = 20$ for *P. achoreum* (Löve and Löve 1956), previously referenced as *P. erectum* by Savage and Mertens (1968), is in error and should be omitted. In addition, the voucher specimen for a count of $2n = 40$ for *P. erectum* (Löve and Löve 1956) cannot be located, bringing the accuracy of this count under question. It also is not included in Table 1.

The count of $2n = 40$ for *P. erectum* ssp. *achoreum* (Löve and Löve 1982) was made from germinating material, which according to A. Löve (pers. comm. 1986) originated from plants of *P. erectum* reported by D. Löve and Bernard (1959) from Otterburne, Manitoba. A specimen deposited in Herbarium Marie-Victorin, Institut Botanique, Université de Montréal, collected by Bernard on August 11, 1958 and determined by D. Löve as *P. erectum* in 1958, matches their 1959 description and is most certainly from the locality from which the seeds were collected. This specimen is, however, referable to *P. ramosissimum* Michx. Until further evidence is obtained attesting that this is not representative of the material counted, the count should be ignored. Therefore, no authenticated chromosome number report exists for *P. erectum*.

D. Phytochemistry

Having found that morphological differences were unsatisfactory to distinguish among eight species of *Polygonum* (almost certainly including *P. achoreum*, although referenced as *P. erectum*), Jones and Mertens (1971) compared paper chromatograms of free amino acids and uncharacterized secondary substances. Free amino acids were similar for all species, and thus of little taxonomic significance. However, chromatographic profiles of the uncharacterized secondary substances were useful for

Table 1. Previously reported chromosome numbers in *Polygonum achoreum* and *P. buxiforme*.

Taxon	2n =	Locality	Reference	Number of collections
<i>P. achoreum</i>	40	Newfoundland	Wolf & McNeill (1987)	3
		Québec	Wolf & McNeill (1987)	4
		Ontario	Wolf & McNeill (1987)	9
		Indiana	Moore et al. (1970)	2
	60	Québec	Wolf & McNeill (1987)	4
<i>P. buxiforme</i>	40	Indiana	Moore et al. (1970)	1
	60	Nova Scotia	Wolf & McNeill (1987)	11
		Nova Scotia	Moore et al. (1970)	4
		New Brunswick	Wolf & McNeill (1987)	17
		Ontario	Wolf & McNeill (1987)	7
		New York	Wolf & McNeill (1987)	8
		Ohio	Wolf & McNeill (1987)	2
		Indiana	Moore et al. (1970)	2

distinguishing the taxa.

Kawasaki *et al.* (1986) determined that quercetin glycosides are the most common foliar flavonoids in the Polygonaceae, with quercitrin (quercetin-3-O-rhamnoside) and quercetin-3-O-glucuronide predominant. The authors also reported that although myricetin glycosides are rare in the family, they comprise the majority of foliar flavonoids in *P. aviculare*.

In their investigation of anthocyanin pigments in 33 species of Polygonaceae, Yoshitama *et al.* (1984) discovered eight cyanidin glycosides, with only cyanidin 3-glycoside characteristic of *P. aviculare*. The authors also found that these anthocyanins exhibited no geographic or seasonal variation. In contrast, the intraspecific variation of flavonoids is well documented in plants (Bohm and Stuessy 1981, Crawford and Smith 1983, Valant-Vetshera 1985), and has been reported in *P. aviculare* (Gasquez *et al.* 1978).

To investigate whether geographic, intraspecific and/or interspecific flavonoid variation exists in *P. erectum* and *P. achoreum*, material from plants collected throughout their ranges, as well as within and between populations, was analyzed for flavonoid content.

E. Migration History

In addition to the question of the taxonomic status of *P. erectum* and *P. achoreum*, another enigmatic issue exists. These two taxa have different geographic origins, and marked changes in their distribution have occurred over this century. Although *P. erectum* was reported by Gray to be present "everywhere" in 1848 and as "common" in 1889, and by Gleason (1952) to be a "common weed", it presently seems to be rare. McNeill and Pryer (pers. comm. 1985), along with other field botanists, have been

unable to relocate classic locations in New England and Ontario during recent field excursions. Conversely, *P. achoreum*, relatively unknown prior to its late description in 1917 is presently ubiquitous. Therefore, the geographical origin and subsequent distribution of these taxa needs to be investigated.

F. Germination studies

Many taxa possess an asymmetric germination strategy, whereby some seeds can germinate much earlier than others. Also, the survival of dormant seeds in the soil varies among taxa. Although several members of the genus *Polygonum* have been included in germination or seed survival studies (Ransom 1935, Witts 1960, Timson 1965, Roberts and Neilson 1980), this information is not available for *P. achoreum* and *P. erectum*. Hence, the periodicity of emergence and the length of time achenes are viable in disturbed and undisturbed habitats is unknown. Therefore, germination studies using achenes obtained from field collections were performed to elucidate whether asymmetric germination patterns exist, and achenes obtained from herbarium collections were used to help assess the minimum length of time a seed bank could persist in the soil. In addition to this information, field observations and results of soil analyses were compared among habitats of *P. erectum* and *P. achoreum*, in order to investigate what factors are responsible for the apparent changes in the distribution of these two taxa.

G. Origin of *P. achoreum*

The late recognition of *P. achoreum*, coupled with its present abundance as a weed, raises the question of its origin. If really distinct from *P. erectum*, it could be an allopolyploid derivative of *P. erectum* and some member of the *P. aviculare* group, such as

the North American native *P. buxiforme*.

Foliar flavonoid profiles have been documented to help distinguish between different ploidy levels in a taxon created by chromosome doubling or the merging of two taxa (Crawford *et al.* 1980, Soltis and Bohm 1986). Determining the ploidy level of *P. erectum* is also necessary to determine whether *P. achoreum* originated as an allopolyploid derivative. Therefore, flavonoid and cytological evidence will support morphological results when addressing the origin of *P. achoreum*.

The relationship between morphology, foliar flavonoid chemistry, and cytology will aid in determining the taxonomic status of these two taxa, their rank, and if distinct at the specific level, will help to shed some light on the origin of *P. achoreum*. Once the taxonomy and origin of these taxa have been clarified, precise ranges can be plotted using available herbarium records and field collections. Furthermore, information from germination and soil results will help to elucidate factors responsible for changes in the distributions of the taxa over this century.

II. METHODS AND MATERIALS

A. Field Studies and Collections

Fifty collections of plants fitting within the circumscriptions of *P. achoreum*, *P. erectum*, and *P. buxiforme* were made in Alberta, Ontario, Québec, Maine, Maryland, Kentucky, and Tennessee during the summer and fall of 1985 and 1986. Plants collected possessed flowers and/or mature achenes, and were used for subsequent morphometric and flavonoid experiments. Plants with elongated, late season achenes were not collected. Voucher specimens for each collection were pressed in the field, and transported back to the laboratory where they were dried. Vouchers will be deposited at DAO. Once pressed, achenes to be used in germination and cytological studies were removed and stored in envelopes. Achenes of additional collections from Alabama, Maryland, Ontario, Tennessee and Virginia were provided by Edwin B. Smith, University of Arkansas, Fayetteville, Arkansas; Steven R. Hill, Clemson University, Clemson, South Carolina; Michael Oldham, Ontario Ministry of Natural Resources, Southwestern Region, London, Ontario; R. Dale Thomas, Northeast Louisiana University, Monroe, Louisiana; and Thomas Wiebolt, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, respectively.

B. Herbarium Specimens

Over 3330 specimen sheets were examined from the following herbaria: A, ALTA, ALU, C, CAN, CM, COLO, DAO, DS, GH, KNK, KY, LAF, MASS, MICH, MO, MOR, MT, MTMG, NCU, NEBC, NHA, NLU, NY, PH, QFA, S, SASK, TENN, UARK, UBC, UC, US, USAS, UVIC, UWO, V, VPI, WIS, and WVA (acronyms according to Holmgren *et al.* 1981).

To augment field collections used in phenetic analyses, representative herbarium specimens of the taxa under study were chosen to represent collections from regions

that I was unable to visit. In addition, only those herbarium sheets with two or more individuals per sheet, or those collections with duplicate sheets were included, so that intrapopulational variation could also be studied.

C. Morphology

I. Characters chosen

To determine phenetic relationships, sixteen vegetative, five floral, and two achene characters were selected on the basis of reports from the literature of distinguishing characters within the group (Blake 1917, Styles 1962, Mitchell and Dean 1978, Wolf and McNeill 1986), and my own observations of characters in the field, greenhouse, and herbarium. These characters were divided into two independent character sets, one consisting of vegetative characters, and the second comprising floral and achene characters (Table 2 and Figure 1). Styles (1962) determined that heterophylly (where two leaves at the same developmental stage on the main stem and branch are of different sizes) and homophylly (where two such leaves are the same size) were useful vegetative characters to distinguish among members of the *P. aviculare* complex in the British Isles. Furthermore, *P. erectum* has been described as heterophyllous, and *P. achoreum* and *P. buxiforme* as homophyllous (Wolf and McNeill 1986). In an attempt to measure heterophylly and homophylly, three leaves, termed a leaf triplet, were measured. A leaf triplet consists of one stem leaf subtending a branch, the first branch leaf, and the stem leaf directly above the point of branching. The first branch leaf and the second stem leaf are developmentally at the same stage, thus comparing their measurements would be indicative of heterophylly or homophylly. The stem leaf subtending the branch serves as a reference point for the other two leaves as well as allowing stem leaves to be compared (Figure 1). Measurements of all characters were taken using a Zeiss binocular microscope with a long-arm stand.

Table 2. List of characters measured in morphometric analyses.
A. Vegetative data set. B. Floral-achene data set.

A. Vegetative data set.

Stem leaf subtending the branch:

1. Leaf length.
2. Distance to the broadest point on the leaf.
3. Leaf width at the widest point.
4. Petiole length measured from the second articulation above the node to the point where the leaf lamina is twice that of the midvein, or where the leaf flares out laterally.

Second stem leaf:

5. Same as 1.
6. Same as 2.
7. Same as 3.
8. Same as 4.

First branch leaf:

9. Same as 1.
10. Same as 2.
11. Same as 3.
12. Same as 4.
13. Stem internode length, represented by a mean value for three consecutive internodes.
14. Branch internode length, represented by a mean value for three consecutive internodes.
15. Ochreae length.
16. Number of veins at base of ochreae.

B. Floral-achene data set.

17. Perianth length.
18. Achene length.
19. Perianth width at the widest point.
20. Achene width at the widest point.
21. Length of the free portion of the perianth.
22. Width of the free inner perianth segment measured above the sinus.
23. Width of the free outer perianth segment measured at the sinus.

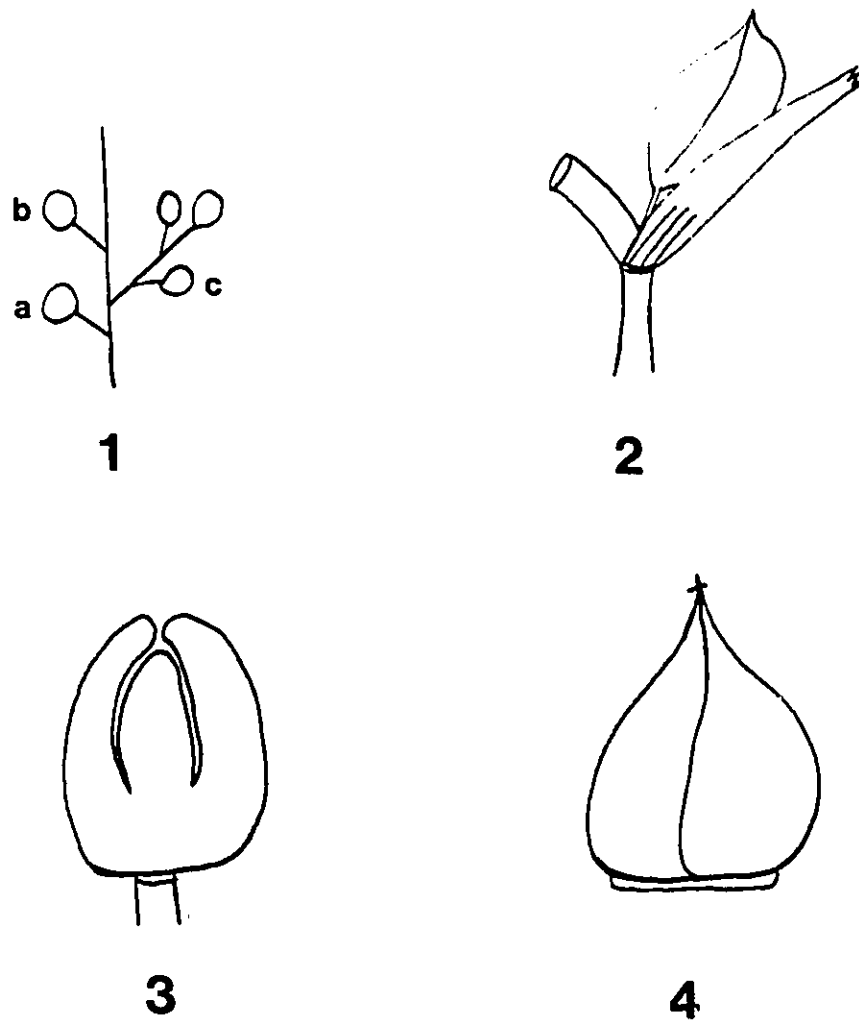


Figure 1. Generalized illustration of characters measured in morphometric analyses. 1a, stem leaf subtending the branch; 1b, second stem leaf; 1c, first branch leaf. 2, ochrea showing veins at base. 3, fruiting perianth. 4, achene.

One hundred and eight individuals from 21 field and 21 herbarium collections, representing the morphological and geographic range of the taxa, were measured (Table 3). To assess the morphological variability within the complex, all characters were scored at the same relative position and developmental stage. At least one leaf triplet and one mature achene were measured per plant and each plant represented one operational taxonomic unit (OTU). Two OTU by character matrices were produced (Appendix 1), one consisting solely of vegetative characters (characters 1-16, Table 2), and the second including only floral and achene characters (characters 17-23, Table 2). Each OTU was assigned a four character code. The first character represents the taxon to which the OTU was tentatively identified (using my own observations and the following keys: Mitchell and Dean 1978, Wolf and McNeill 1986). The second, third, and fourth character represents the population, plant, and achene or leaf triplet, respectively.

Each matrix was inspected initially to assess normality using the S199 summary statistic program of the Engineering and Statistical Research Institute of Agriculture Canada, Ottawa (1981 edition). For all characters, the coefficients of skewness (g_1) and kurtosis (g_2) did not depart significantly from zero and no subsequent transformations were thought necessary. Summary statistics including means, and standard deviations, were also obtained from this program.

To remove the effects of variation in one variable that could be considered to be determinable by that in another (e.g. size effects), regression of certain characters against others (Table 4) was carried out. The residuals of the regressed characters are orthogonal to the regression line, and hence are uncorrelated with the characters used to construct the line (Neff and Marcus 1980). Therefore, the relative variation represented by residuals meets the basic definition of a shape variate because the size of a character relative to another character reflecting overall size can be estimated

Table 3. List of collections used in numerical analyses
(see representative specimens for collection details).

J. Nagy 8 (AC); *J.M. Gillette & D.A. Mitchell* 4037 (DAO); *S.R. Downie & D.S. Katz* 750 (DAO); *H. Groh* 2929 (DAO 306897); *E.H. Moss* 6644 (UBC); *J.A. Calder & D.B.O. Saville* 10388 (DAO); *J.H. Hudson* 2244 (DAO); *B. Boivin, F.L. LeFort et J.G. Vaillancourt* 11600 (DAO 146452, UBC 155407); *W. Krivda* 1596 (DAO 146446); *D.S. Katz* 335, 339, 356, 360, 363, 368, 430, 479 - 481, 488, 510 (DAO); *D.S. Katz & M.J. Oldham* 476 (DAO); *D.S. Katz, S. Rooney & M. Rasmussen* 493 (DAO); *L.L. Consaul & L. Goodfellow* 718 (OTT); *W.G. Dore & E. Gorham* 45.895 (DAO 306974, QFA 251464); *J.H. Christ & W.W. Ward* 14980 (NY); *W.A. Weber* 15475 (COLO 330334, 330335); *K. Thorne* 3929 (NY); *J.F. Brenckle* 37-01 (US 1826755, 1826756), 38-02 (GH, DAO 306869); *J.W. Thieret* 33614 (LAFF 5119); *R. McVaugh* 12761 (MICH); *R.D. Thomas & J. Berry* 97883 (DAO); *T.F. Wieboldt* 6118 (DAO); *L.C. Wheeler* 5660 (DAO 306862, MICH, PH, WIS); *H.E. Ahles* 85330 (AC, NEBC); *D.E. Boufford & E.W. Wood* 23152 (WIS); *F.T. McFarland* 52-A (NY, TENN, UC, WVA).

Table 4. List of characters measured in morphometric analyses with residual values.

Stem leaf subtending the branch:

1. Leaf length.
2. Distance to the broadest point on the leaf relative to character 1.
3. Leaf width at the widest point relative to character 1.
4. Petiole length relative to character 1.

Second stem leaf:

5. Leaf length relative to character 1.
6. Distance to the broadest point of the leaf relative to character 5.
7. Leaf width at the widest point relative to character 5.
8. Petiole length relative to character 5.

First branch leaf:

9. Leaf length relative to character 1.
10. Same as 2.
11. Leaf width at the widest point relative to character 9.
12. Same as 4.
13. Stem internode length.
14. Branch internode length.
15. Ochreae length.
16. Number of veins at base of ochreae.
17. Perianth length.
18. Achene length.
19. Perianth width at the widest point relative to character 17.
20. Achene width at the widest point relative to character 18.
21. Length of the free portion of the perianth relative to character 17.
22. Width of the free inner perianth segment measured above the sinus.
23. Width of the free outer perianth segment measured at the sinus.

(Reist 1985).

Residual values were calculated in order to express length relative to width in characters such as leaves, perianths and achenes, and length of the fused portion of the perianth relative to the total length (Table 4). Residuals were also calculated to measure heterophylly and homophylly in order to express the length and width of the second stem and first branch leaves and petioles relative to each other, as well as in relation to the first stem leaf. The vegetative and floral-achene data matrices were each subjected to an analysis of variance (ANOVA) using vegetative and achene measurements as individuals, and plants as populations, to determine whether residual values provided more information than their raw data counterparts. Comparing F values among the groups of plants, residual values for 14 characters having F values with a probability of $F > 0.0001$, replaced their corresponding raw data values in both the vegetative and floral-achene data matrices (Table 4).

To ensure that every character contributed equally to subsequent multivariate tests, characters in the vegetative and floral-achene data matrices were standardized to zero mean and unit standard deviation. However, if close correlation among characters exists, standardization can emphasize noise and decrease separation of OTU's. To investigate this, unstandardized and standardized vegetative and floral-achene data matrices were subjected to Principal Component Analysis (PCA) using SAS (SAS Institute Inc. 1985), to determine which data set accounted for the greatest variance on the first principal component (PC) axis (a covariance matrix was used with pre-standardized data). Unstandardized data matrices for each of the vegetative, and floral-achene data sets were chosen. These unstandardized matrices were combined into one OTU by character matrix using values for plant means only. Therefore, each OTU represents a mean of other OTU's measured from the same plant. Each OTU is now represented by a three character code indicating the taxon, population, and plant,

respectively. This data matrix was used in all ensuing numerical analyses and is presented in Appendix 2.

ii. Data reduction

ANOVA was performed using individuals as OTU's and populations as groups to select characters that would be useful to differentiate populations in further analyses as relatively few variables may be needed to display patterns of data or differentiate among taxa. Ten characters (1, 7, 11, 15-18, 20-23; Table 4) with F values having a probability of $F > 0.0001$ were retained in the data set.

iii. Numerical methods employed

CLUSTRIT (S075) Cluster Analysis package of Agriculture Canada (Lefkovitch 1981) was used to run two hierarchical clustering methods: the unweighted pair group method using averages (UPGMA), and the flexible sort method with $\alpha = 0.625$ and $\beta = -0.25$ (Lance and Williams 1967). To assess distances between pairs of OTU's, the Gower distance coefficient (Gower 1971), a metric similarity measure that standardizes data by range, was used for all characters in each cluster method. Ordination techniques, including PCA (using variance-covariance matrices) and Canonical Variate Analysis (CVA; using Mahalanobis distance between centroids), were employed using programs available in SAS.

D. Flavonoid Chemistry

Thin-layer chromatography (TLC), which enables the detection of flavonoids using small amounts of plant material, was used in a preliminary examination to determine if

foliar flavonoid profiles differed amongst 19 individuals from seven field collections and their greenhouse progeny. Flavonoids were extracted from 0.01 - 0.015 gm of ground leaf material per plant following the procedure of Classen and Nozzolillo (1981), and the extracts spotted on polyamide plastic-backed plates. Quercetin, kaempferol, rutin, naringen, and chlorogenic acid standards were run alongside the unknown samples.

Plates were run in the first dimension in an aqueous solvent (water: pyridine: cyclohexanone, 90:5:5), followed by an organic solvent (n-butyl acetate: methanol: formic acid: water, 60:30:5:5) in the second dimension (Classen and Nozzolillo 1981). Plates were dried and viewed under UV light (366 nm) before and after spraying with a flavone reagent in water containing 1 % triethylamine (Classen and Nozzolillo 1981). Foliar flavonoid profiles of 52 individuals from 49 field and greenhouse collections were then compared to assess intrapopulational variation and differences between field and greenhouse material using the modified procedures of Isobe *et al.* (1980). Once taxa were delimited from morphometric analyses, their respective profiles could be compared.

For each collection 1.5 - 5.0 gm of ground leaf and stem material from each individual were covered with approximately 100 mL of 70 % ethanol and left overnight. This mixture was filtered through Whatman No. 1 paper and the filtrate flash evaporated (*in vacuo*) until dry using a water bath at 75°C. This extract, containing the flavonoids, was re-suspended in approximately 20 mL of 10 % methanol, filtered again, and spotted on Whatman No. 1 chromatography paper (23 x 18 cm) with the edges pinked to allow for overflow of the solvents. To compare flavonoid profiles, chromatograms were run in both one and two dimensions. The organic solvent used was 1-butanol: glacial acetic acid: water (BAW, 4:1:5, upper organic phase), and the aqueous solvent contained 15 % glacial acetic acid (HOAc; Mabry *et al.* 1970). For two dimensional chromatograms, the first dimension was run in the organic solvent, and

the second dimension run in the aqueous solvent. The following flavonoids, obtained from Isobe, were used as standards: quercetin-3-O-glucoside, quercetin-3-O-glucoside-2"-gallate, quercetin-3-O-rhamnoside; quercetin-3-O-rhamnoside-2"-gallate, kaempferol-3-O-glucoside-2"-gallate, and myricetin-3-O-glucoside. All spots were viewed under UV light (366 nm) before and after treating with ammonium vapour. Ammonium vapour enhances the colour of the spots by producing a colour change of structural importance, and also aids in the detection of minor spots (Markham 1982). R_f values in BAW, HOAc, and water (H_2O) were calculated for the unknowns and the standards. Further structural identification of unknowns was not made due to time limitations.

E. Cytology

Mitotic chromosome counts from root tips were made using modified techniques of Mertens (1969). Actively growing root tips were removed from plants grown in the University of Ottawa greenhouse and prefixed in a 0.002 M 8-hydroxyquinoline (0.058 g in 200 mL water) solution for three hours at 5°C. After rinsing in distilled water, root tips were fixed in absolute ethanol: glacial acetic acid (3:1) for a minimum of one hour, and then rinsed and stored in 70 % ethanol at 5°C. Prior to squashing, fixed root tips were hydrolyzed for 45 minutes in 5N HCL at room temperature (20 - 22°C).

Slides were made semi-permanent by ringing the cover slip with a melted mixture of gum mastic: paraffin wax (1:1), or clear nail polish. Chromosomes were examined and counted using a Leitz Dialux 20 EB microscope, and photographed with a Zeiss Universal microscope using Ilford XPI 400 film and Numarski optics. A voucher slide for each collection examined will be deposited at DAO.

F. Germination Studies

i. Achene stratification

To overcome the problem of dormancy known to occur in *P. erectum* (Justice 1941) and other members of the Section *Polygonum* (Ransom 1935, Justice 1941, Wits 1960, Timson 1965), achenes from field and herbarium collections (Table 5) were stratified as follows. The persistent perianth surrounding the achene was manually removed by rubbing the achene between the thumb and forefinger. Achenes were subsequently surface sterilized by soaking in a 1.5 % Javex solution for twenty minutes, rinsed twice with distilled water, and placed in Fisher 100 x 15 mm sterile plastic petri dishes between Whatman No. 1 filter paper circles moistened with distilled water. Petri dishes were then sealed with PARAFILM and placed in the dark at $7^{\circ} \pm 1^{\circ} \text{C}$ for a period of eight weeks.

ii. Achene treatment prior to germination

The effects of three pre-treatments on achene germination were examined. Achenes were either left unscarified, were scarified manually by sanding lightly with 80 grade 3M sandpaper, or had their pericarps removed under a Zeiss binocular microscope using forceps and a dissecting needle. All achenes were surface sterilized, and stratified as above.

iii. Achene germination

To facilitate germination, petri dishes were placed 22.0 - 26.5 cm beneath VITA LIGHT (3830) double cathode and power twist lights on carts with height adjustable shelves for 16 hours a day at a light intensity of 25 watts/m² (measured with a Kettering

Table 5. Collections used in germination studies
(see representative collections for voucher details).

Taxon	Voucher
<i>P. achoreum</i>	<i>R. Whittmann</i> 771 (COLO 7640, 332011, NY); <i>D.S. Katz</i> 324 - 327, 329, 331 - 333, 367, 368 (DAO); <i>L.L. Consaul</i> 725, 726 (OTT); <i>S. De Stefano</i> 285 (WIS); <i>R. Brooks</i> 13578 (MO 2690589, NY); <i>W.A. Weber</i> 15475 (COLO 330334, 330335), 154978 (COLO 331969); <i>J. Wingate</i> 3368 (COLO 403888).
<i>P. erectum</i>	<i>D.S. Katz</i> 339, 354, 360 (DAO); <i>R. Kral</i> 49957 (NCU 446669); <i>G.F. Buddell II & J.W. Thieret</i> 2384 (NCU 521603); <i>S.R. Hill</i> 10787 (MICH); <i>T.F. Wieboldt, C.A. Stevens & A.B. Davenport</i> 4535 (CAL); <i>M.J. Oldham & J.P. Prevett</i> 4118 (UTM 650233).

45 radiometer model 65) in the University of Ottawa greenhouse. Achenes were left to germinate for up to one month. Once germination began, the top piece of filter paper was removed to increase the amount of light reaching the emerging radicles.

iv. Seedling care

To distinguish between genetic and environmentally induced traits, plants from all collections were grown under comparable environmental conditions. After the third pair of true leaves developed, plants were transplanted to plastic pots (6.0 cm long by 4.0 cm wide by 5.0 cm high). These pots were surface sterilized with a dilute Javex solution, filled with Premier 98 % organic potting soil with a 5 mm layer of sand on the bottom, and placed 12 - 14 cm beneath VITA LIGHTS. Plants were fertilized every two weeks with Rx-15-30-15 brand fertilizer (15 % nitrogen, 30 % phosphoric acid, 15 % soluble potassium), and sprayed twice weekly with DEXOL brand pesticide to control European Red Mite (*Panonychus ulmi* Koch) and Greenhouse White Fly (*Trialeurodes vaporariorum* Westwood). These cultivated plants were used in subsequent cytology and flavonoid chemistry experiments. Representative specimens of these cultivated plants will be deposited at DAO.

v. The tetrazolium viability test

To determine whether any of the taxa studied showed asymmetric germination, scarified and unscarified achenes that failed to germinate within one month following stratification were tested for viability using the tetrazolium test (Gabe 1970, as cited by de Bezada 1981). Achenes were covered with a 1 % solution of 2,3,5-triphenyl tetrazolium chloride (TTC; 1 gram of TTC in 100 mL distilled water, pH 6-8), and placed in the dark at 35° C for seven hours to allow absorption of the stain. After staining, the

pericarp and seed coat were removed with forceps under a Zeiss binocular microscope, and the colour of the internal cotyledon tissue was recorded: a red stain is the mark of viability, whereas a light pink or no stain is the mark of non-viability.

vi. Phenology

Over 1200 plants cultivated in the greenhouse, representing 42 collections, provided information regarding time to flower initiation, and plant height at flowering. The time to initiate flowering is defined as how long following germination a plant takes to produce at least one flower. An outbreak of powdery mildew (*Erysiphe* sp.) killed many plants, including those that had not yet flowered, causing the experiment to terminate 10 weeks after germination. Results therefore, represent the average number of weeks to flower for 43 % of the plants grown. An ANOVA was performed to determine whether the means of the taxa for time to flower initiation, and plant height at flowering differed significantly at the 0.0001 % level.

G. Soil Analyses

In order to compare habitats of the taxa, soil analyses were performed. From the top 5 cm of soil, 100 - 200 g samples were removed at each of the 18 collection sites. Measurements of pH and conductivity (Micro MHO/ug) were determined in the field using Hertsau E588 pH and E587 conductivity meters with a 1:1 soil to water ratio (Bower and Wilcox 1965). Once air dried, 20 - 40 grams of soil per sample were used to perform particle size analysis using the hydrometer method (Day 1965, Savage 1981). In an effort to determine soil texture (percent sand, clay, silt). Five to seven grams of soil per sample were used for the extraction of calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K) using the mild extractant, ammonium hydroxide. These mineral

extracts were analyzed by atomic absorption using flame spectroscopy with a Varia AA-17 (Page *et al.* 1982). Mineral extraction values are expressed as parts per million (ppm). All particle size and mineral analyses were performed by Mr. John Loop, Department of Geology, University of Ottawa.

An ANOVA using each soil sample as an OTU, and sites referable to each taxon as groups, was performed to determine whether the means of collection sites of each taxon for mineral contents, pH, or conductivity differed significantly.

III. Results

A. Morphology

One hundred and eight field and herbarium collections were scored for 23 characters, 14 of which were represented by residuals obtained after regression against other variables. An ANOVA, using OTU's as individuals and populations as groups, found 10 characters to have F values with $P < 0.0001$, and were used in subsequent cluster analysis, PCA, and CVA.

The phenogram resulting from UPGMA (Figure 2) indicates three clusters of OTU's at the 0.60 phenon level. Three clusters of OTU's are also apparent in the phenogram obtained from the flexible sort clustering ($\alpha = 0.0625$, $\beta = -0.25$) at a phenon level of 1.10 (Figure 3). Although the three clusters in both the UPGMA and the flexible sort phenograms contain the same OTU's, differences in the clustering of OTU's at lower phenon levels exist due to the different properties of each clustering method. UPGMA which is a relatively weak clustering method, conserves the original multidimensional space such that the inter-group measures are unchanged after groups are formed (Lance and Williams 1967). In the flexible sort method, as the value for β tends toward zero the clustering becomes space-dilating and OTU's are grouped more intensely (Lance and Williams 1967, Sneath and Sokal 1973).

The first two PC axes accommodated 69 % of the total variation within the data set, with the remaining eight PC axes each representing 8.5 % or less of the total variation. Plotting component scores of the first two PC axes gives clear group separation (Figure 4). Five characters contributed greatly to the total variance on the first PC axis. In decreasing order of importance, these characters were: width of the inner perianth segment, length of the first stem leaf, number of veins at the base of the

Figure 2. Phenogram of 108 OTU's produced by UPGMA clustering.

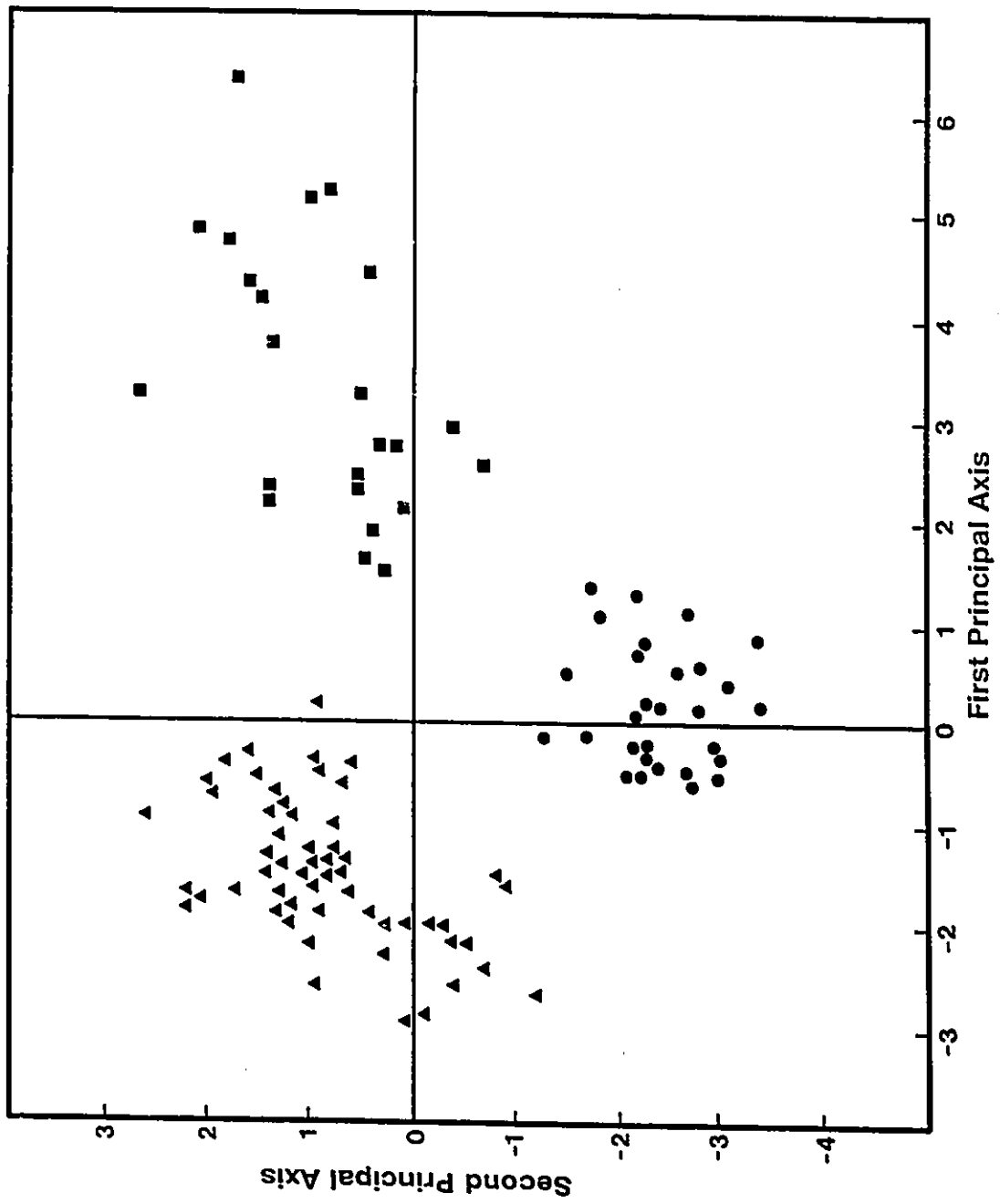
- ▲ - *P. achoreum*
- - *P. buxiforme*
- - *P. erectum*

Figure 3. Phenogram of 108 OTU's produced by the flexible sort clustering ($\beta=0.0625$, $\alpha=-0.25$).

- ▲ - *P. achoreum*
- - *P. buxiforme*
- - *P. erectum*

Figure 4. Principal component ordination of 108 OTU's showing distribution along first two axes.

- ▲ - *P. achoreum*
- - *P. buxiforme*
- - *P. erectum*



ochreae, length of the free portion of the perianth relative to the length of the achene, and width of the outer perianth segment.

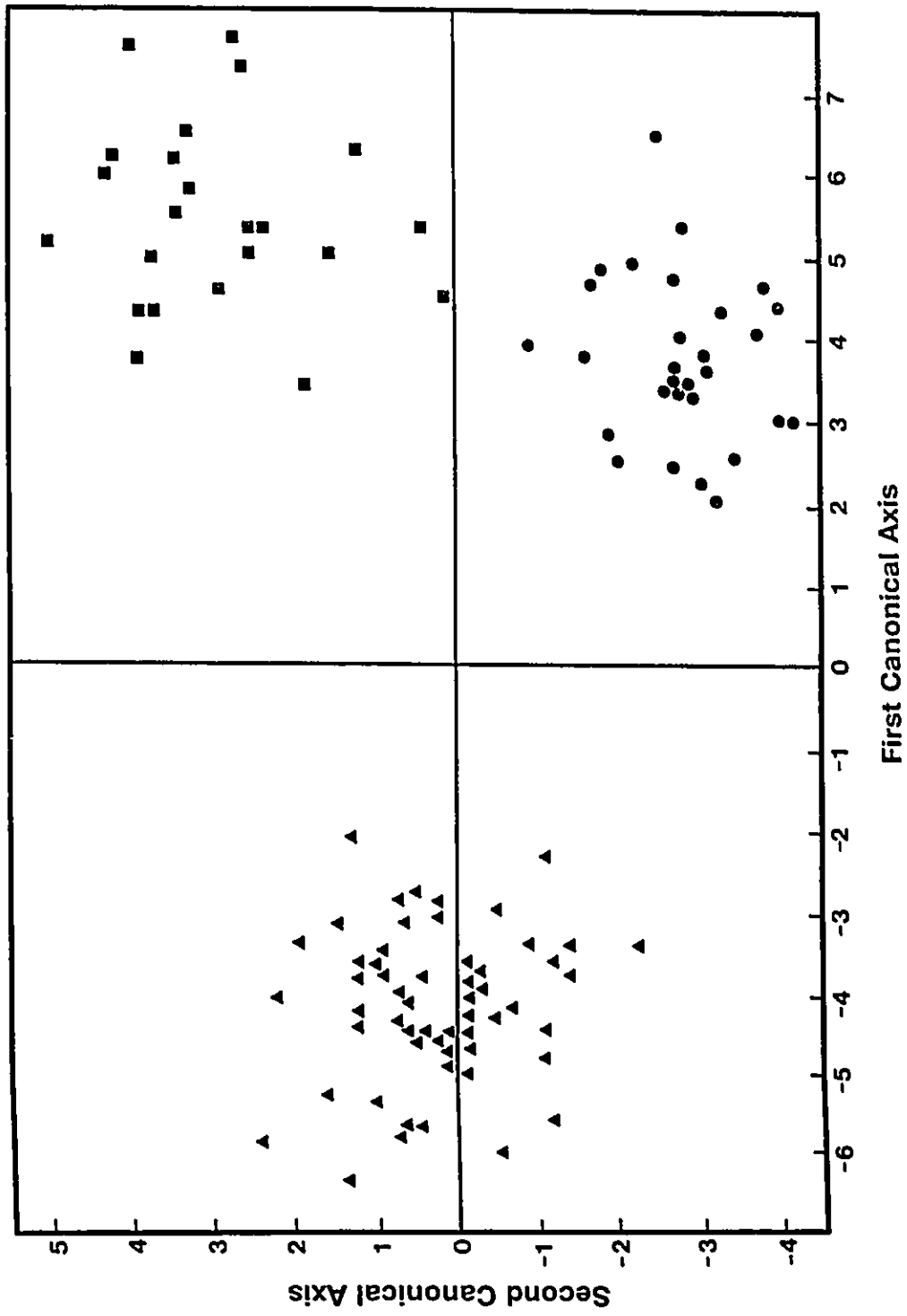
Four characters having high loadings on the second PC axis are, in order of decreasing importance: achene length, leaf width relative to the length of the branch and second stem leaves (indicative of heterophylly and homophylly), and perianth length.

Results from cluster and ordination methods, where no *a priori* grouping is assumed and character weighting is not employed, suggest three distinct groups. Using CVA, these three groups were designated *a priori* as separate, and tested to see whether they are indeed so. The Mahalanobis distance (D2) between each group or centroid, are significantly different at the 0.0001 % level indicating that the three groups are distinct. Plotting the first canonical variate axis, which represents 82 % of the total variation between groups, with the second canonical variate axis graphically displays OTU's in each of the three groups (Figure 5). Only perianth characters have high loadings on the first canonical variate axis: width of the inner perianth segment, perianth length, length of the inner perianth segment relative to the perianth length, and width of the outer perianth segment. Characters with high canonical loadings associated with the second canonical variate axis are: ochreae length, width of the inner perianth segment, width of the outer perianth segment, and number of veins at the base of the ochreae.

Three identical groups were obtained from cluster analysis, PCA, and CVA. In addition to the 10 characters that best distinguished the groups, two qualitative characters, achene colour and distribution of papillae over the achene surface, have been used by Wolf and McNeill (1986) to distinguish members of the Section *Polygonum*. However, these characters were not included in the numerical analyses because they contributed more to the inter-OTU distance matrix than any single or

Figure 5. Canonical variate ordination of 108 OTU's showing distribution along first two axes.

- ▲ - *P. achoreum*
- - *P. buxiforme*
- - *P. erectum*



continuous character. Instead these characters are incorporated as key characters in the taxonomy section.

Type specimens and/or type descriptions of *P. achoreum*, *P. erectum*, and *P. buxiforme* were compared with the suite of characters best distinguishing the groups. Each group was readily associated with one of these types, hence the groups symbolized by ▲, ● and ■ are referable to *P. achoreum*, *P. buxiforme*, and *P. erectum*, respectively.

B. Flavonoid Chemistry

Results from TLC and paper chromatography experiments were similar. No variation was found between field and greenhouse collections from the same population. Although a different flavonoid profile characterized each taxon, there was no evidence of variation among or within populations of the same taxon. The collections examined for flavonoid content in both TLC and paper chromatography methods are listed in Table 6.

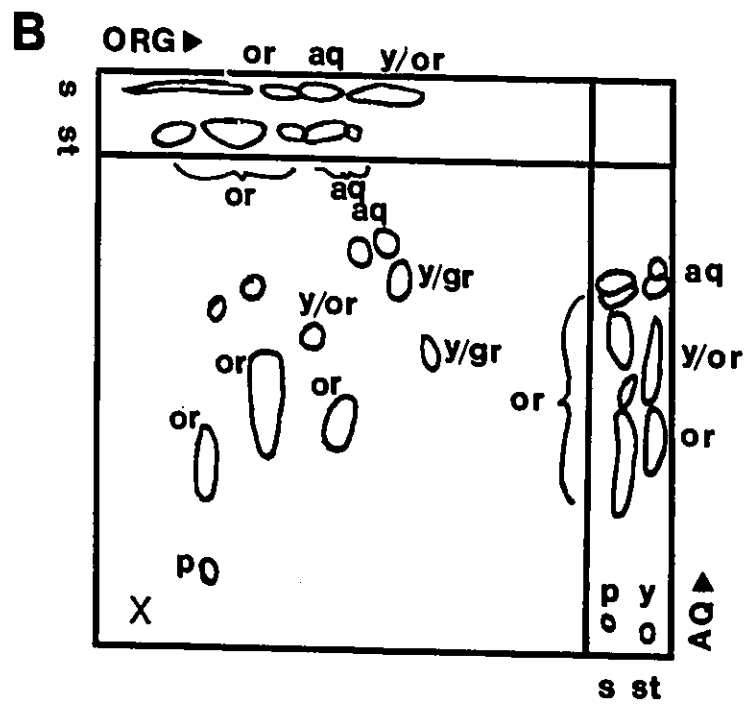
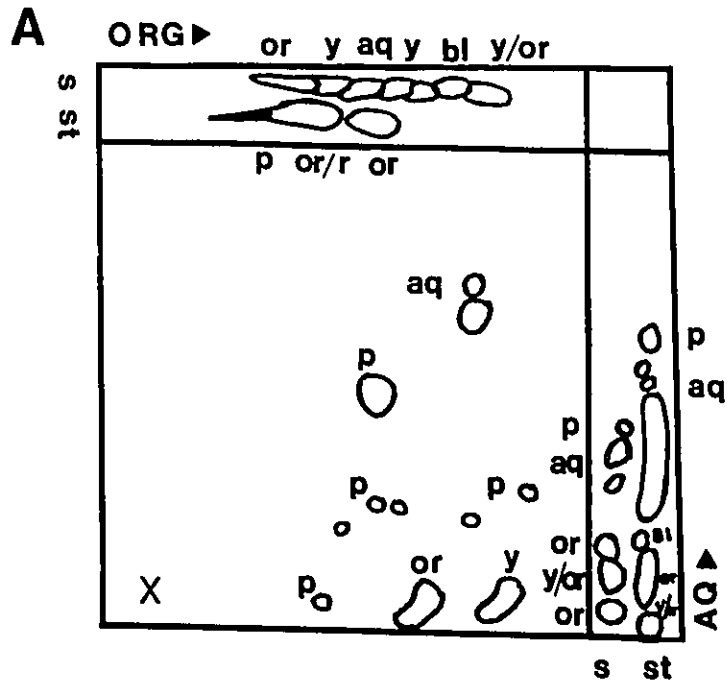
A TLC chromatogram for each taxon, showing both one (with standards) and two dimensions was photographed under UV light (360 nm) after spraying with the flavone reagent and is represented in Figure 6. The one dimensional paper chromatograms for each taxon are illustrated in Figure 7, and the chromatographic data are presented in Table 7. Eight flavonoids were isolated from 24 collections of *P. achoreum*, 12 collections of *P. erectum*, and 13 collections of *P. buxiforme*.

Flavonoids are most useful for distinguishing taxa at the species level (in association with morphological and other types of data), and have helped elucidate the origin of hybrids. Intraspecific polyploids derived from genomic doubling can be identified on the basis of similar profiles between progeny and their parents, whereas

Table 6. List of collections used in flavonoid analysis
(see list of representative specimens for collection details).

Taxon	Voucher
<i>P. achoreum</i>	ONTARIO: <i>D.F. Brunton</i> 6188 (DAO); <i>L.L. Consaul & L. Goodfellow</i> 718, 721, 726 (OTT); <i>D.S. Katz</i> 367 (DAO); <i>D.S. Katz & M.J. Oldham</i> 468 (DAO); MAINE: <i>D.S. Katz, S. Rooney & M. Rasmussen</i> 494 - 496 (DAO). QUÉBEC: <i>D.S. Katz</i> 326, 332, 429, 444, 446, 447, 479 - 482, 487, 489 (DAO). ALBERTA: <i>S.R. Downie & D.S. Katz</i> 750, 751.
<i>P. buxiforme</i>	ONTARIO: <i>D.S. Katz</i> 334, 336, 366, 369, 430, 451, 459, 460, 476 (DAO). MAINE: <i>D.S. Katz,</i> <i>S. Rooney & M. Rasmussen</i> 497 (DAO).
<i>P. erectum</i>	ONTARIO: <i>M.J. Oldham & J.P. Prevett</i> 4118 (CAN). MARYLAND: <i>S.R. Hill</i> 10787 (NY); <i>D.S. Katz</i> 339 (DAO). KENTUCKY: <i>D.S. Katz</i> 356, 357 (DAO). TENNESSEE: <i>D.S. Katz</i> 360, 363 (DAO); <i>R.D. Thomas, S. Thomas & J. Berry</i> 97883 (DAO); <i>R.D. Thomas, S. Thomas & L. Thomas</i> 97886 (DAO). VIRGINIA: <i>T.F. Wieboldt</i> 6118 (DAO).

Figure 6. Representation of TLC plates for standards and flavonoids of *P. achoreum* (A), *P. buxiforme* (B) and *P. erectum* (C). Perimeter of plate represents unidirectional migration of sample (s) and standards (st). Centre of plate represents two dimensional chromatogram of sample, x=origin. Colour characterization: aq=aqua, bl=black, gr=green, or=orange, p=purple, r=red, y=yellow.



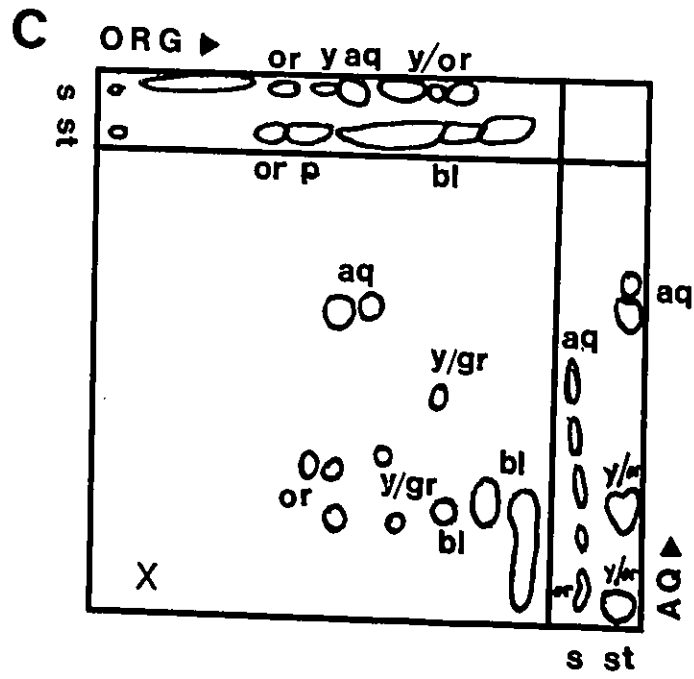


Figure 7. Representative paper chromatogram for standards and the flavonoids of *P. achoreum* (A), *P. buxiforme* (B) and *P. erectum* (C). Compounds 9 - 14 refer to standards. Characterization of all flavonoid compounds is presented in Table 7.

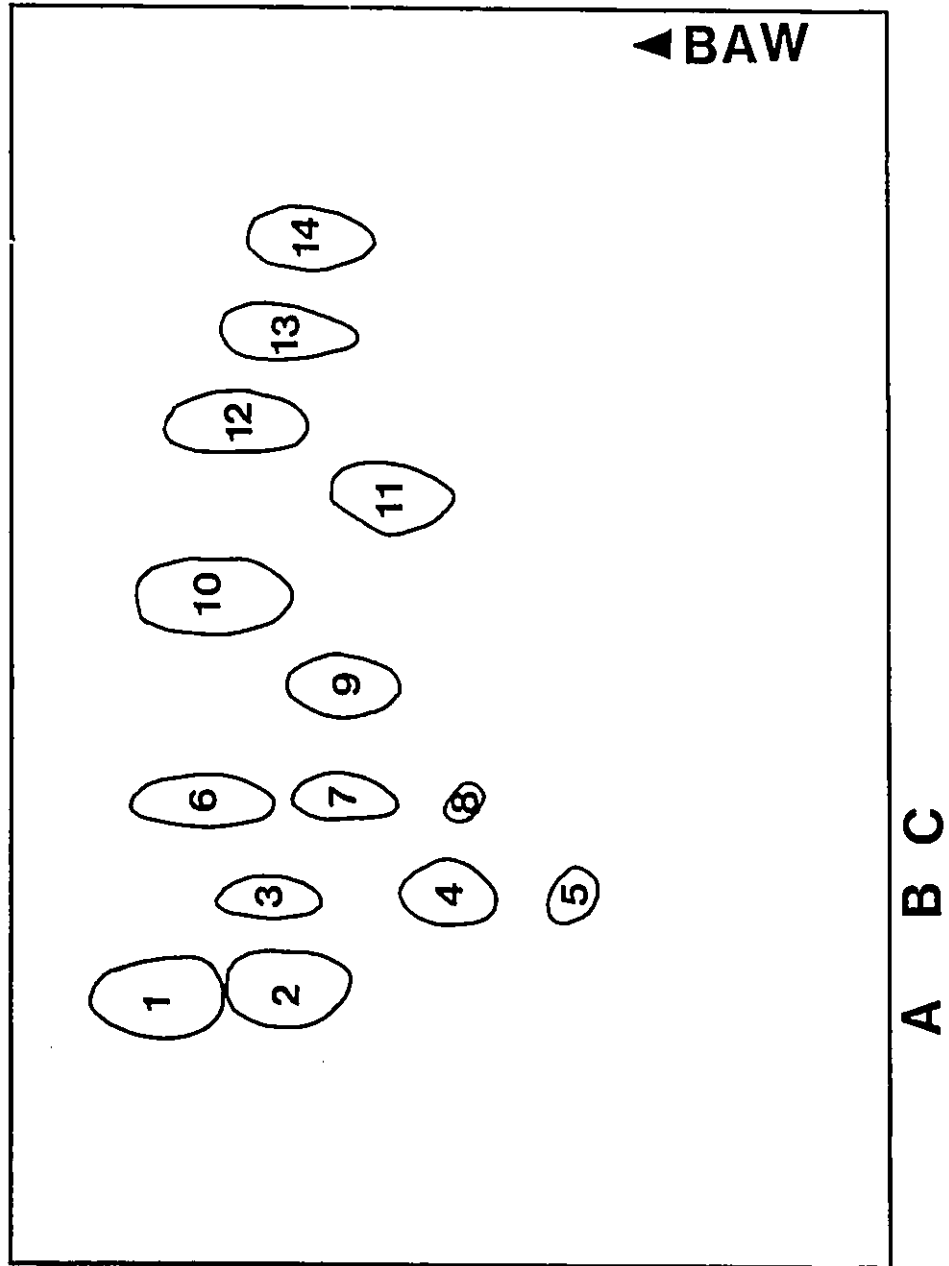


Table 7. Paper chromatographic and Rf data.

A. *Polygonum achoreum*, *P. buxiforme*, and *P. erectum*.

Taxon	Compound	Rf's X 100			Colours at 350 nm	
		BAW	HOAc	H ₂ O	UV	UV/NH ₃
<i>P. achoreum</i>	1	39			O	O
	2	32	26	14	O	O
<i>P. buxiforme</i>	3	35			O	O
	4	25	29	18	O	O
	5	19	21	8	O	O
<i>P. erectum</i>	6	39			BL	BL
	7	31	37	29	BL	BL
	8	24	27	14	BB	BPB

Colour key: O = Orange, BB = Bright - Blue, BPB = Bright Purple - Blue, BL = Black.

B. Standards

Standard	Compound	Rf's X 100		
		BAW	HOAc	H ₂ O
Quercetin 3-glucoside	9	31	21	7
Quercetin 3-rhamnoside	10	38	27	13
Quercetin 3-glucoside- 2"-gallate	11	28	22	10
Quercetin 3-rhamnoside- 2"-gallate	12	36	17	3
Kaempferol 3-glucoside- 2"-gallate	13	34	25	11
Myricetin 3-rhamnoside	14	33	25	13

interspecific hybridization results in the production of novel compounds or summation of profiles (Crawford *et al.* 1980). Results indicate that each taxon has a unique profile which does not vary across their geographic ranges, corroborating results from morphometric analyses that *P. achoreum*, *P. erectum*, and *P. buxiforme* are distinct taxa. Although identification of compounds is necessary before adequate comparisons among taxa can be made, results indicate that *P. achoreum* did not originate as an allopolyploid derivative of *P. erectum* and *P. buxiforme*.

C. Cytology

Somatic chromosome numbers have been obtained for ten populations of *P. achoreum*, *P. buxiforme*, and *P. erectum* (Table 8). All counts were multiples of the basic chromosome number, $x = 10$.

P. achoreum

Chromosome counts for three populations were all $2n = 40$, agreeing with those previously reported by Moore *et al.* (1970) and Wolf and McNeill (1987).

P. buxiforme

The one collection examined was $2n = 60$, confirming previous reports by Moore *et al.* (1970), and Wolf and McNeill (1987).

P. erectum

Thirteen counts from three populations of *P. erectum* were all $2n = 40$, and are reported here for the first time (Plate 1). This tetraploid level for *P. erectum* does not deviate from other ploidy levels reported for the section.

Table 8. Chromosome counts and voucher specimen list for
P. achoreum, *P. buxiforme* and *P. erectum*
 (see list of representative specimens for details).

Taxon	2n =	Voucher
<i>P. achoreum</i>	40	<i>D.F. Brunton</i> 6188 (DAO); <i>L.L. Consaul & L. Goodfellow</i> 726 (OTT); <i>D.S. Katz</i> 325, 336, 367 (DAO).
<i>P. buxiforme</i>	60	<i>D.S. Katz</i> 430 (DAO).
<i>P. erectum</i>	40	<i>D.S. Katz</i> 339, 354, 360 (DAO); <i>S.R. Hill</i> 10787 (NY).

Plate 1. Mitotic chromosome squash of a root tip cell in *P. erectum*
($2n=40$).



Because *P. achoreum* has the same or a higher ploidy level (Wolf and McNeill (1987) also report one hexaploid population) than *P. erectum*, an allopolyploid origin is scarcely possible. Furthermore, morphological and flavonoid differences do not support a hybrid origin for *P. achoreum*.

D. Germination Studies

i. Achene pre-treatments

The effects of three pre-treatments on achene germination in *P. achoreum* and *P. erectum* prior to stratification were examined. Pre-treatments included: unscarified achenes, scarification by sanding, and pericarp removal.

Achenes with their pericarps removed exhibited abnormal germination. The hypocotyl instead of the radicle emerged first, no roots developed and death resulted. Scarified achenes demonstrated an average 12 % decrease in germination compared to unscarified achenes (Table 9). These results suggest that manual scarification by sanding and pericarp removal decreases germination, and that cold stratification alone is adequate to break dormancy in achenes of *P. achoreum* and *P. erectum*.

ii. Achene viability

Achenes from herbarium collections were found to retain their viability for as long as 14 years. Consequently, a seed bank could persist in the soil for extended periods of time. Achenes from field collections which did not germinate after one month were tested for viability using the tetrazolium test, all were nonviable, implying there is no periodicity of germination under these conditions. However, knowing that a seed bank could persist in the soil, achenes which would periodically be brought to the surface of

Table 9. Relationship between number of achenes sown and percent germination for three treatments of achenes from *P. achoreum* and *P. erectum*.

Treatment	Taxon	Number of achenes sown	Number germinated	Percent germinated
Unscarified	<i>P. achoreum</i>	100	44	44
	<i>P. erectum</i>	27	9	33
Scarified	<i>P. achoreum</i>	53	17	32
	<i>P. erectum</i>	27	4	15
Pericarp removed	<i>P. achoreum</i>	16	0	0
	<i>P. erectum</i>	6	0	0

the soil as a result of a disturbance such as flooding, trampling, plowing, etc. would, presumably, be able to germinate.

iii. Phenology

Greenhouse propagated plants were similar to their naturally occurring parents. Plants grew best when kept moist and were generally more robust and branched when potted individually as opposed to potting many plants together. *Polygonum achoreum* initiated flowers earlier and at lower heights than *P. erectum*. The average time to flower initiation and the height at flowering for *P. achoreum* was 6 weeks (± 1 day) at 5 cm (± 0.05 cm), and for *P. erectum*, 8 weeks (± 1 day) at 20.6 cm (± 0.05 cm). A list of collections used, and an OTU by character matrix which includes plant height at flowering and number of weeks to initiate flowers is presented in Appendix 3. An ANOVA, using mean height values and mean number of weeks to flower initiation for populations as OTU's, and taxa as groups, demonstrated that the means for flower initiation and plant height at flowering differs significantly between the two taxa at the 0.0001 % level. These results agree with different flowering dates observed in the field: *P. achoreum* flowers from May to November while *P. erectum* flowers from July to October.

E. Field Observations

The ranges of *P. erectum* and *P. achoreum* are separate, yet overlap in Essex County, Ontario, and according to herbarium records, in Du Page County, Illinois. However, in these areas, these taxa have not been found growing together, and are separated by at least two kilometers. Differences were evident in habitats of *P. erectum* and *P. achoreum*. *Polygonum erectum* sites were partially shaded, disturbed, and were

primarily located close to a source of water (streams or rivers), although, in Ontario, plants were found in drier habitats. Populations were localized and rare, and averaged 10 plants per site. Plants of *P. achoreum* were found in open, disturbed areas such as sidewalks, roadsides, field entrances, vacant lots, and building sites. Populations were widespread and common, averaging 20 plants, and generally consisted of more plants than in *P. erectum* populations.

Morphological variation was apparent among vegetative characters in field collections of each taxon examined. In mesic habitats, plants of both taxa were robust, reaching a height of 40 - 50 cm. In drier habitats, plants referable to *P. erectum* were slender, unbranching, and had extremely reduced leaves. Mowed or trampled habitats are common to both taxa, and plant size was reduced accordingly. Stem and branch internodes became shorter, and the leaves smaller. *Polygonum erectum* did not seem to compete well with other species in several habitats, but at some of these sites, mowing provided sufficient disturbance to maintain the population.

F. Soil Analyses

Soil texture, mineral content, conductivity and pH were compared from 19 collection sites of *P. achoreum* and *P. erectum* (Table 10). *Polygonum achoreum* sites were of three soil textures: sandy loam, sandy clay loam, and sandy clay. *Polygonum erectum* sites included six soil textures: clay, clay loam, sandy clay loam, silty clay loam, sandy loam, and loam. Although a limited number of sites for each taxon was sampled, results suggest that both taxa are found in sandy loam and sandy clay loam soils, and that plants of *P. erectum* occupy a broader range of soil textures with distinct clay elements.

To compare mineral content, pH, and conductivity between the taxa, an ANOVA

Table 10. Soil collection sites and data for soil parameters. A. Soil texture. B. Mineral content, pH and conductivity. Samples 1-12 and 13-19 represent *P. achoreum* and *P. erectum* sites respectively.

A. Percent sand, clay, silt and soil texture.

Sample Number	Site	% Sand	% Clay	% Silt	Soil Texture
1.	D.S. Katz 324	45.5	36.0	18.5	Sandy Clay
2.	D.S. Katz 329	73.8	18.0	8.2	Sandy Loam
3.	D.S. Katz 333	75.0	17.5	7.5	Sandy Loam
4.	D.S. Katz 367	57.5	20.0	22.5	Sandy Clay Loam
5.	D.S. Katz 368	68.8	15.2	16.0	Sandy Loam
6.	D.S. Katz 482	78.4	17.4	4.2	Sandy Loam
7.	D.S. Katz 483	55.1	31.2	13.7	Sandy Clay Loam
8.	D.S. Katz 489	58.3	25.2	41.5	Sandy Clay Loam
9.	D.S. Katz 494	62.5	17.5	20.0	Sandy Clay Loam
10.	D.S. Katz 495	62.5	21.8	15.7	Sandy Clay Loam
11.	S.R. Downie & D.S. Katz 751	75.0	15.2	9.8	Sandy Clay Loam
12.	S.R. Downie & D.S. Katz 752	52.0	23.0	25.0	Sandy Clay Loam
13.	D.S. Katz 340	28.4	27.2	44.4	Clay Loam
14.	D.S. Katz 354	55.0	27.0	18.0	Sandy Clay Loam
15.	D.S. Katz 355	57.5	18.7	23.8	Sandy Loam
16.	D.S. Katz 356	19.9	38.7	41.4	Silty Clay Loam
17.	D.S. Katz 360	42.6	22.0	35.4	Loam
18.	D.S. Katz 363	63.8	20.0	16.2	Sandy Clay Loam
19.	D.S. Katz & M.J. Oldham 461	25.7	41.7	32.6	Clay

B. Mineral content, conductivity and pH.

Sample Number	Ca ppm	Mg ppm	Na ppm	K ppm	Conductivity Micro MHO/ug	pH
1.	2435	76	41	92	360	7.9
2.	790	21	4	115	65	7.0
3.	1329	39	7	45	65	7.6
4.	1274	39	18	78	150	7.6
5.	1775	39	62	67	275	7.6
6.	858	19	26	65	290	7.5
7.	2532	172	18	96	79	8.0
8.	2502	121	15	118	265	7.5
9.	2013	31	93	57	590	7.6
10.	1616	26	45	65	580	7.1
11.	2362	313	63	292	1300	7.0
12.	1177	68	396	128	402	8.3
13.	2623	87	35	175	205	7.0
14.	888	49	3	201	125	7.2
15.	1556	50	16	46	155	6.8
16.	1429	237	16	197	102	6.8
17.	2045	108	7	118	225	6.7
18.	2079	61	4	95	225	6.5
19.	1914	116	8	182	78	7.7

was performed. The means for Na and pH differed significantly between *P. achoreum* and *P. erectum* at the 0.05 % and 0.001 % level respectively. Sodium values were higher for *P. achoreum* sites and averaged 66 ppm, ranging from 4 - 396 ppm; with *P. erectum* values averaging 13 ppm and ranging from 3 - 35 ppm. *Polygonum achoreum* sites tended to be more alkaline, with an average pH of 7.6 and range of 7.0 - 8.3, whereas *P. erectum* sites, averaging 7.0 and ranging from 6.5 - 7.7, were neutral to alkaline. Although several populations of both taxa were found in sandy loam and sand clay loam soils, sites of *P. achoreum* had higher sodium levels. Many of these *P. achoreum* sites were near paved roads, and the higher sodium concentrations could be a result of winter road salting.

IV. DISCUSSION AND CONCLUSIONS

Three groups of taxa have been delimited morphologically using cluster analysis, PCA, and CVA. Comparing these groups to type specimens and/or type descriptions the names *Polygonum achoreum*, *P. erectum*, and *P. buxiforme* could readily be assigned. Foliar flavonoid profiles of each taxon were found to be unique and invariant geographically. *Polygonum achoreum* and *P. erectum* have different ecological requirements. Data from plants grown in the greenhouse show that *P. erectum* and *P. achoreum* differ phenologically; flowering dates also differ in the field.

The morphological - geographical species concept (Davis and Heywood 1963) is the most pragmatic approach to species recognition. A biosystematic investigation, which pools together information from cytology, morphology, phytochemistry, phytogeography, etc., is necessary to fulfill this concept. However, Davis and Heywood (1963) clearly state that the species recognized must be delimitable by morphological attributes. In addition to being morphologically distinct, data from flavonoid chemistry, cytology, phenology, and geographic distribution (to be discussed) indicate that *P. achoreum* and *P. erectum* are separated by a number of discontinuous independent character differences which satisfies the requirements of this model. Therefore, specific rank for each taxon is warranted. Löve and Löve's (1982) treatment of *P. achoreum* as a subspecies of *P. erectum*, and Mertens and Raven's (1965) placement of *P. achoreum* under synonymy with *P. erectum*, are rejected. With regard to *P. buxiforme*, results from morphological, cytological, and flavonoid investigations dispel any confusion concerning the misidentification of this taxon with *P. achoreum*.

Since morphological, cytological, and flavonoid chemistry results do not support the allopoloid origin of *P. achoreum* from *P. erectum* and *P. buxiforme*, *P. achoreum* may have been introduced into North America during the early part of this century. To determine the origin, range and migration history of *P. achoreum*, herbarium collection

records were mapped with date of collection (Figures 8 - 12). Only two collections of *P. achoreum* have been made outside of North America (Hult  n.1968). Both of these are from Denmark, collected in 1899 and 1925 from waste places at Svendbourg Harbour and the steam-mill on the Island of Fyen, respectively. With no recent account of this taxon in Denmark, it is presumed that these records represent casual introductions and that it no longer occurs there; hence Denmark is not included as part of the range of *P. achoreum*. All nineteenth century collections are from midwestern North America (Figure 8), the species first being collected in Saskatchewan by Bourgeau in 1857 while on Palliser's British North America expedition (Spry 1968). These early records centered in midwestern North America and the exclusion of records outside of North America suggests that *P. achoreum*, although not recognized as distinct until Blake described it in 1917, is endemic to this continent and not introduced as has been suggested. The migration history of *P. achoreum* during this century is illustrated in Figures 8 to 12. At present, *P. achoreum* ranges from British Columbia east to Newfoundland, and from the Northwest Territories south to Colorado.

Conversely, mapping collection records of *P. erectum* shows a decrease in range and abundance over this century (Figures 13 - 17). In the nineteenth century, *Polygonum erectum* was well established from midwestern to northeastern US and southern Ontario (Figure 13). Only single collections of *P. erectum* are available from Colorado, Nebraska, and Qu  bec; the most recent being from 1899. With no collections made during this century, *P. erectum* may now be extinct in these areas. Between 1900 and 1949 (Figures 14 and 15), the range of *P. erectum* receded eastward, and between 1950 and 1974 (Figure 16), it receded southward. At present, *P. erectum* seems to be rare and is known only from several southeastern states, Illinois, Missouri, and southern Ontario (Figure 17).

Although the possibility exists that the actual distribution history of the taxa can be

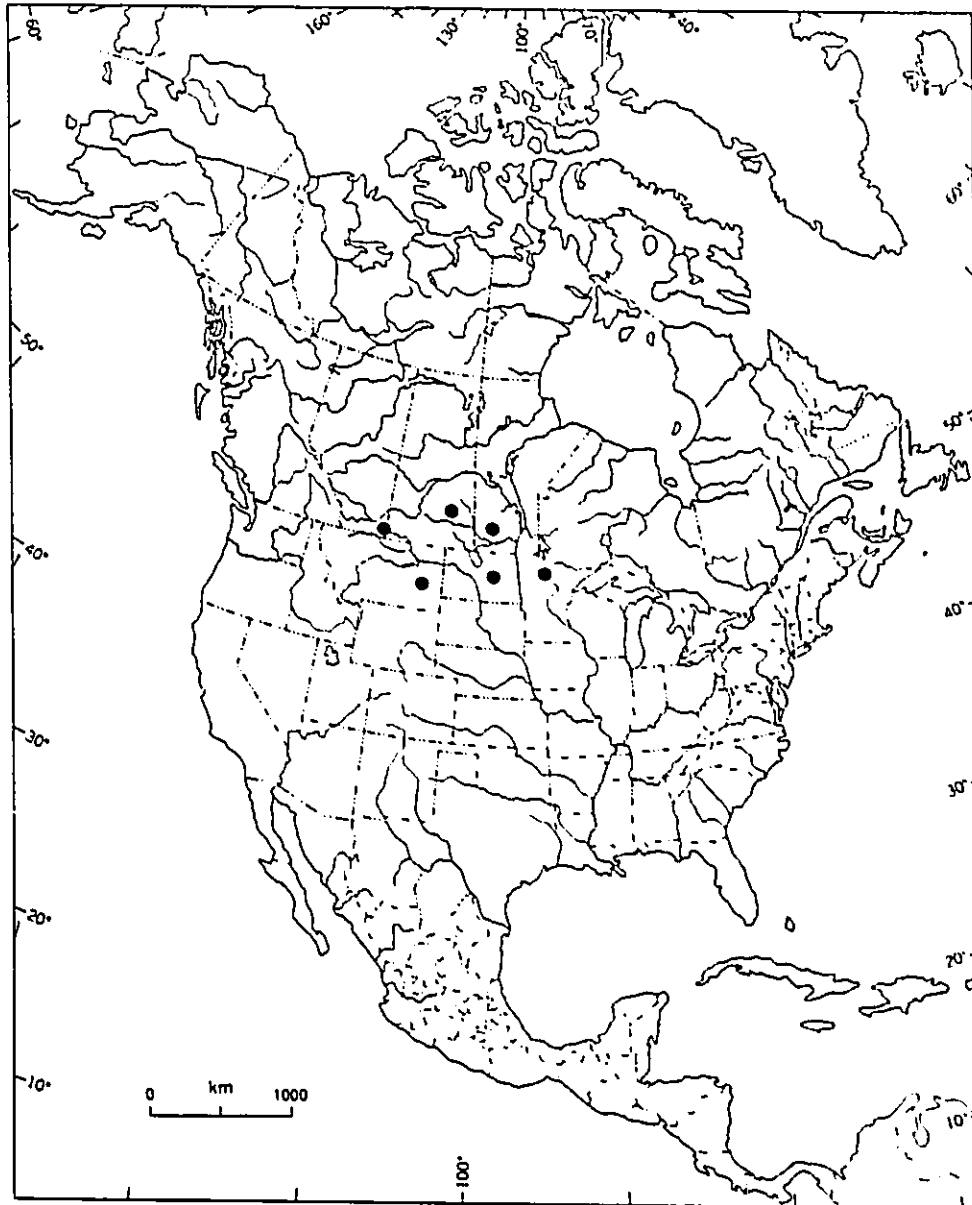


Figure 8. Collection records of *P. achoreum* before 1900 mapped by state and province.

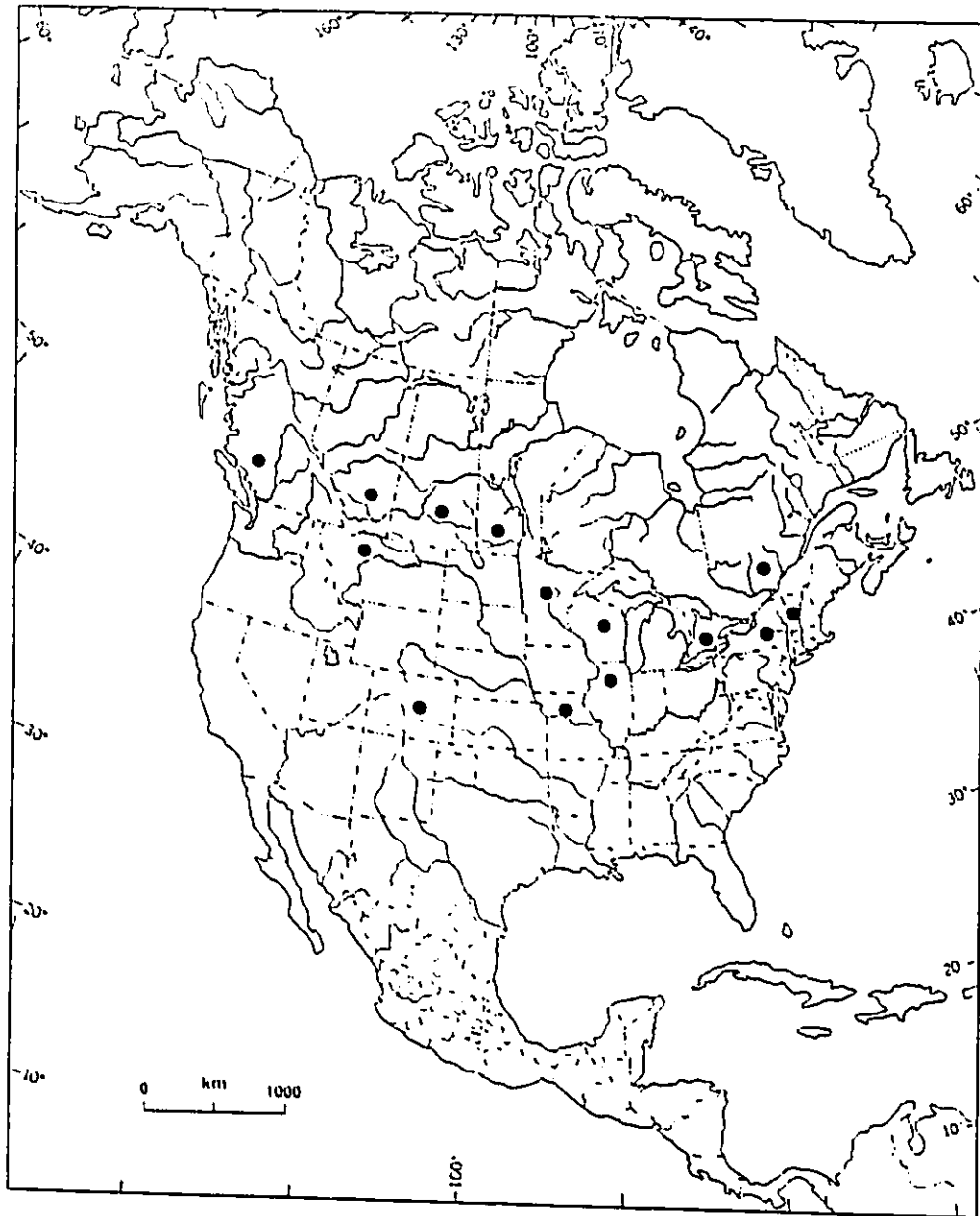


Figure 9. Collection records of *P. achoreum* between 1900 and 1924 mapped by state and province.

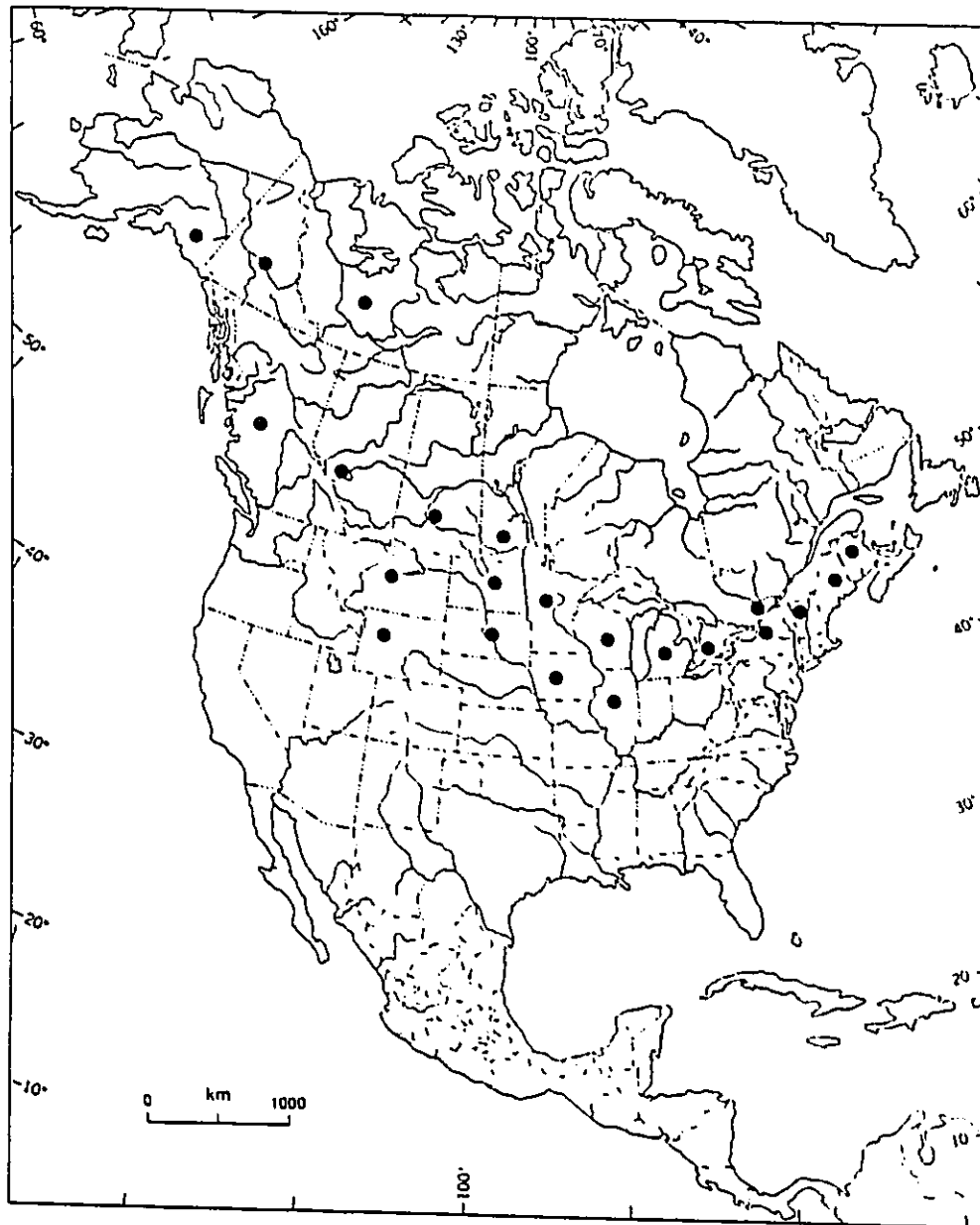


Figure 10. Collection records of *P. achoreum* between 1925 and 1949 mapped by state and province.

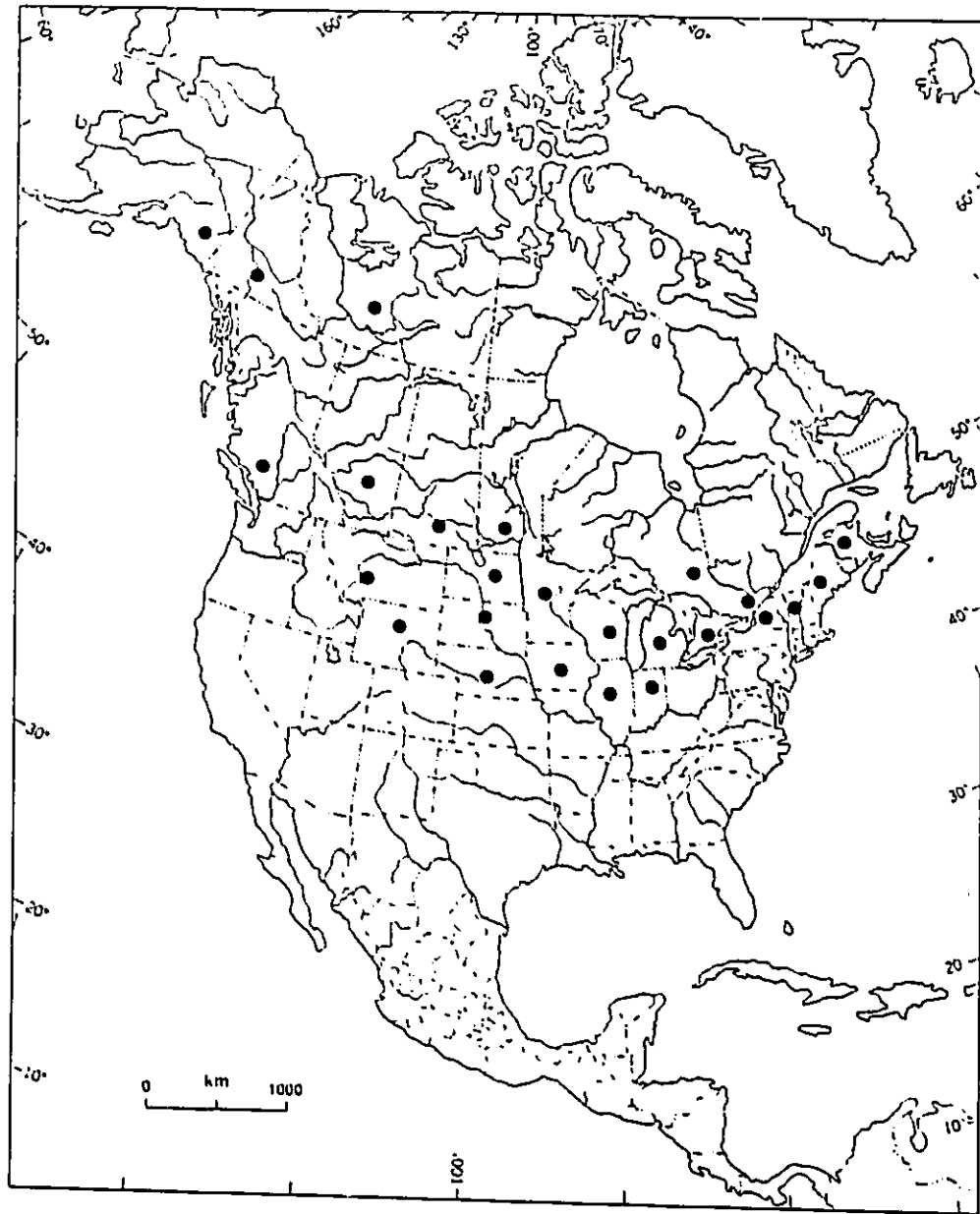


Figure 11. Collection records of *P. achoreum* between 1950 and 1974 mapped by state and province.

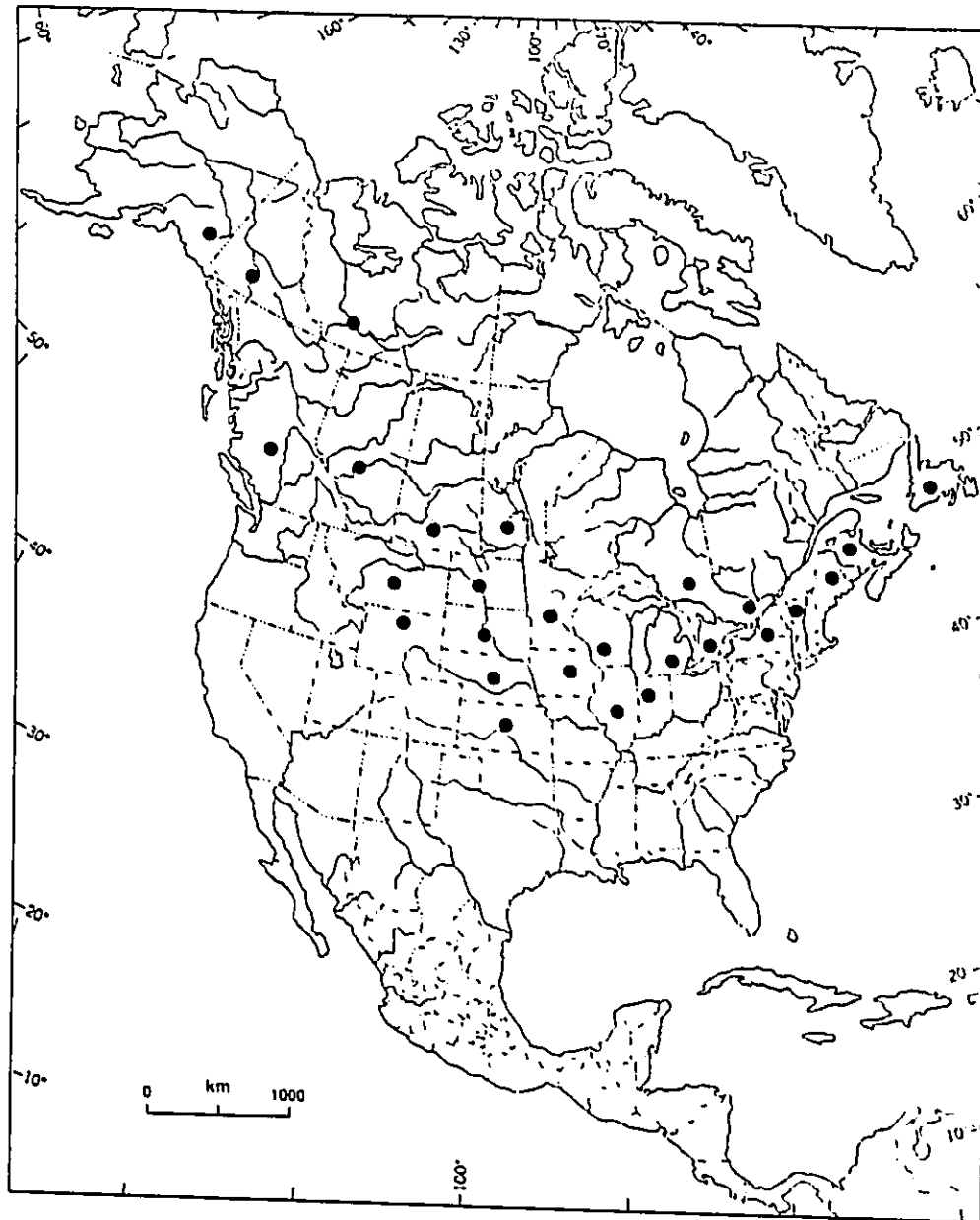


Figure 12. Collection records of *P. achoreum* between 1975 and 1987 mapped by state and province.

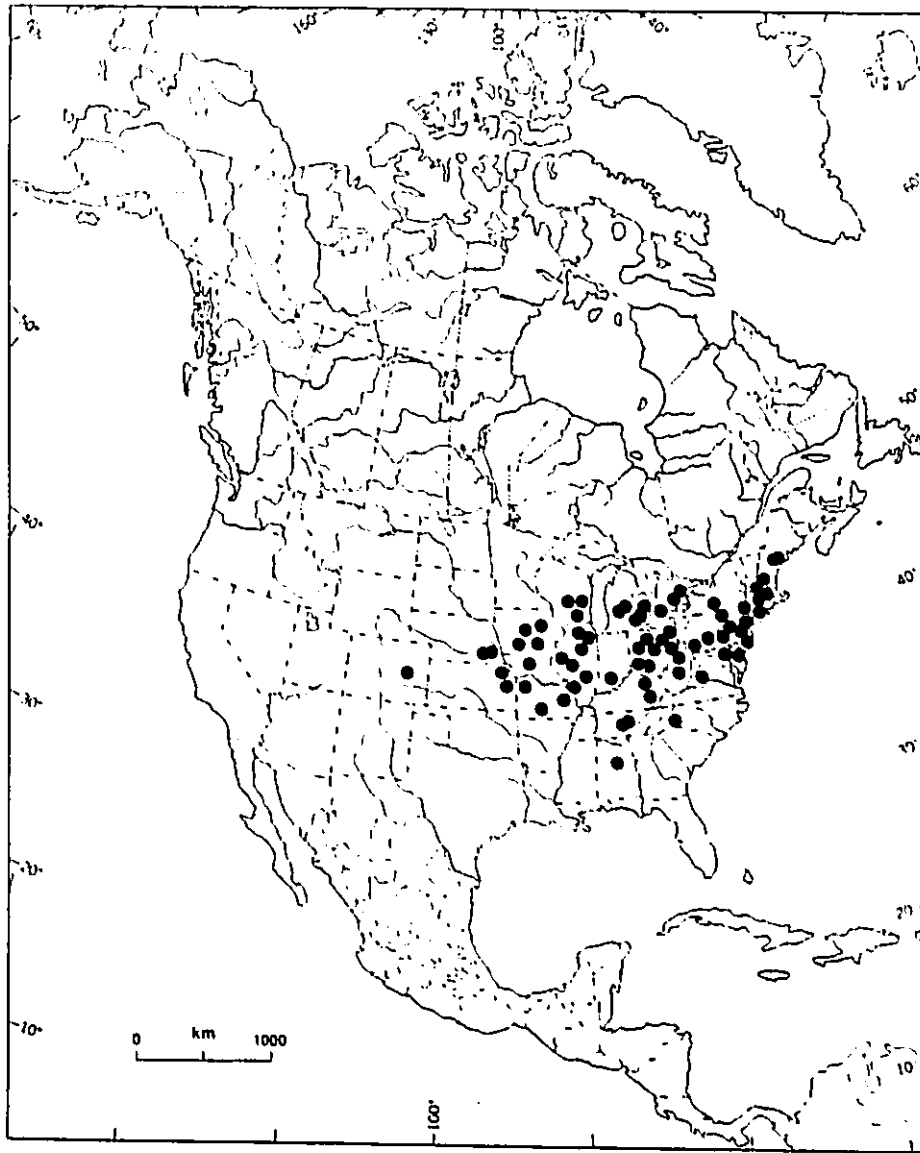


Figure 13. Distribution of *P. erectum* before 1900.

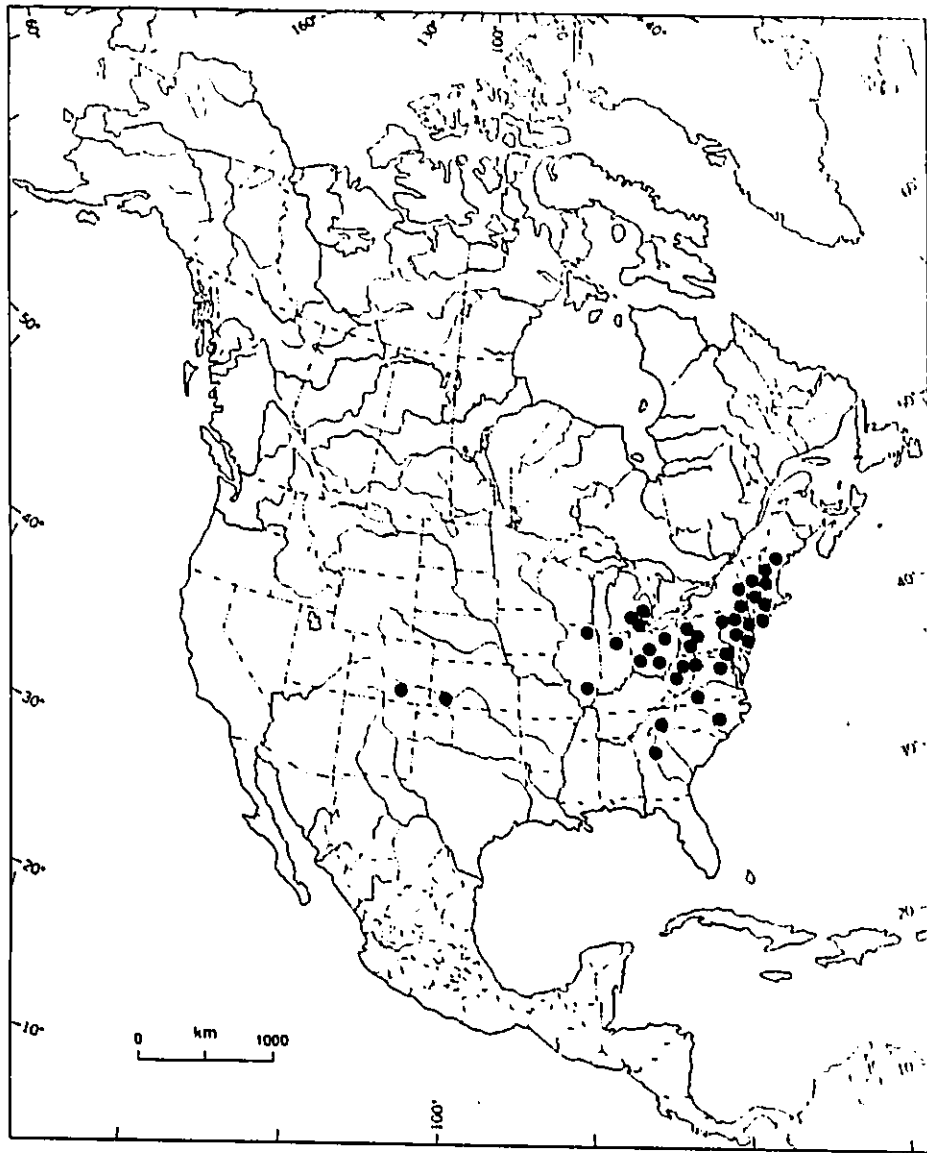


Figure 14. Distribution of *P. erectum* between 1900 and 1924.

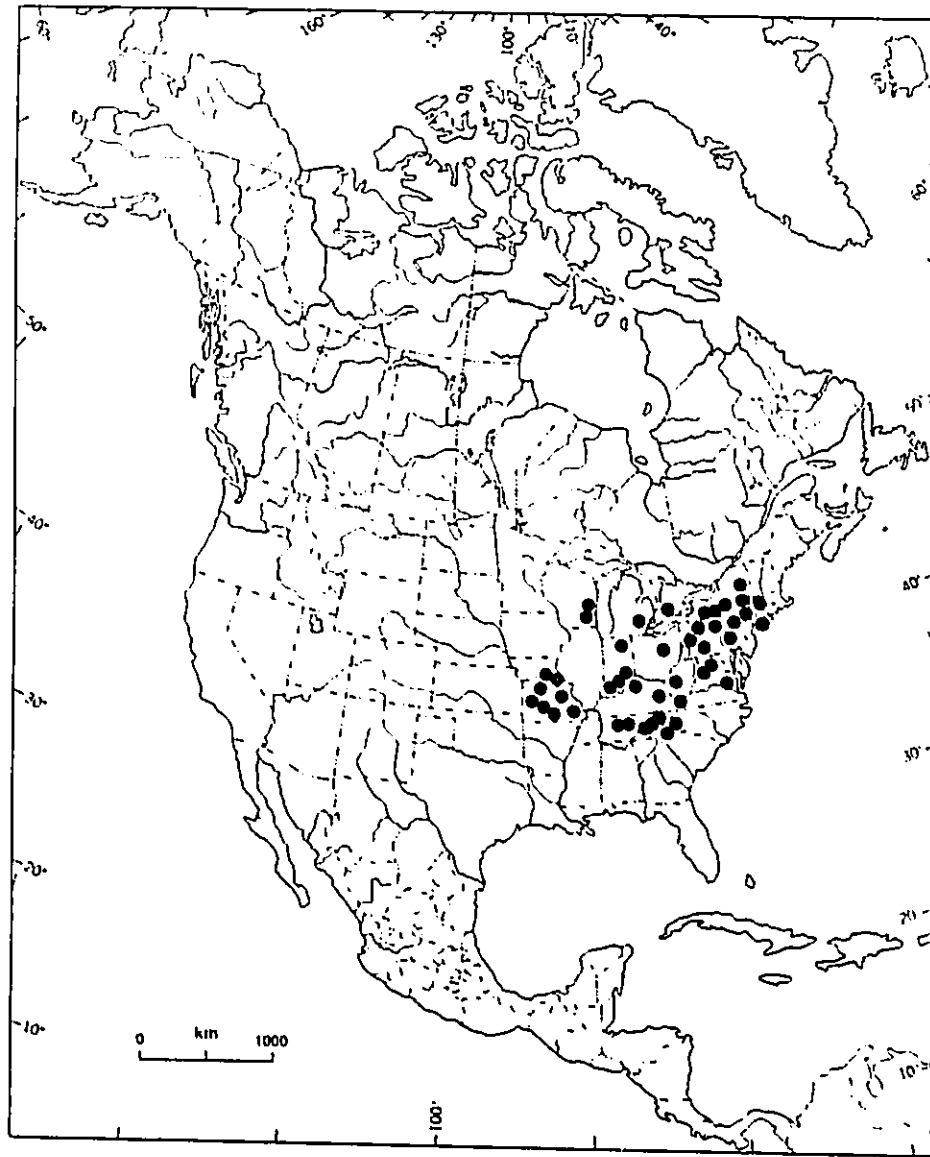


Figure 15. Distribution of *P. erectum* between 1925 and 1949.

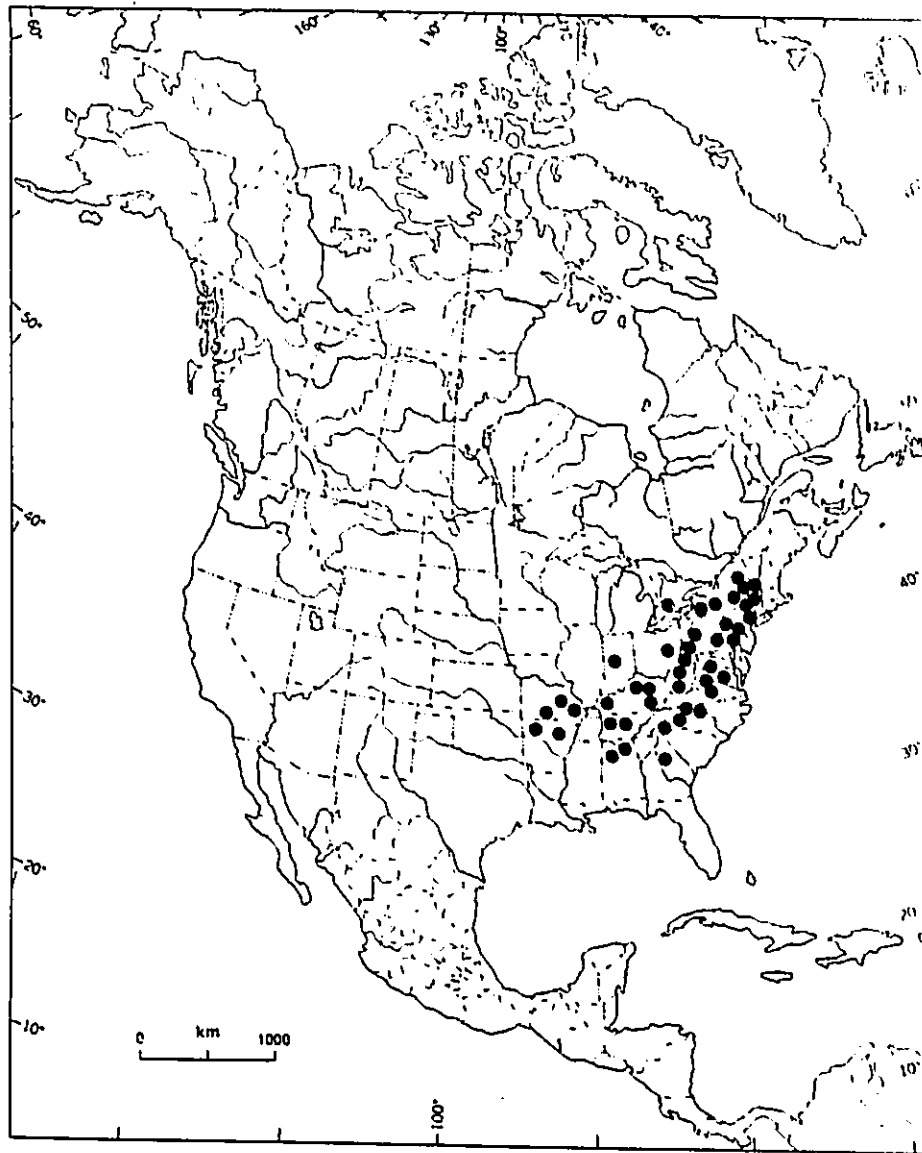


Figure 16. Distribution of *P. erectum* between 1950 and 1974.

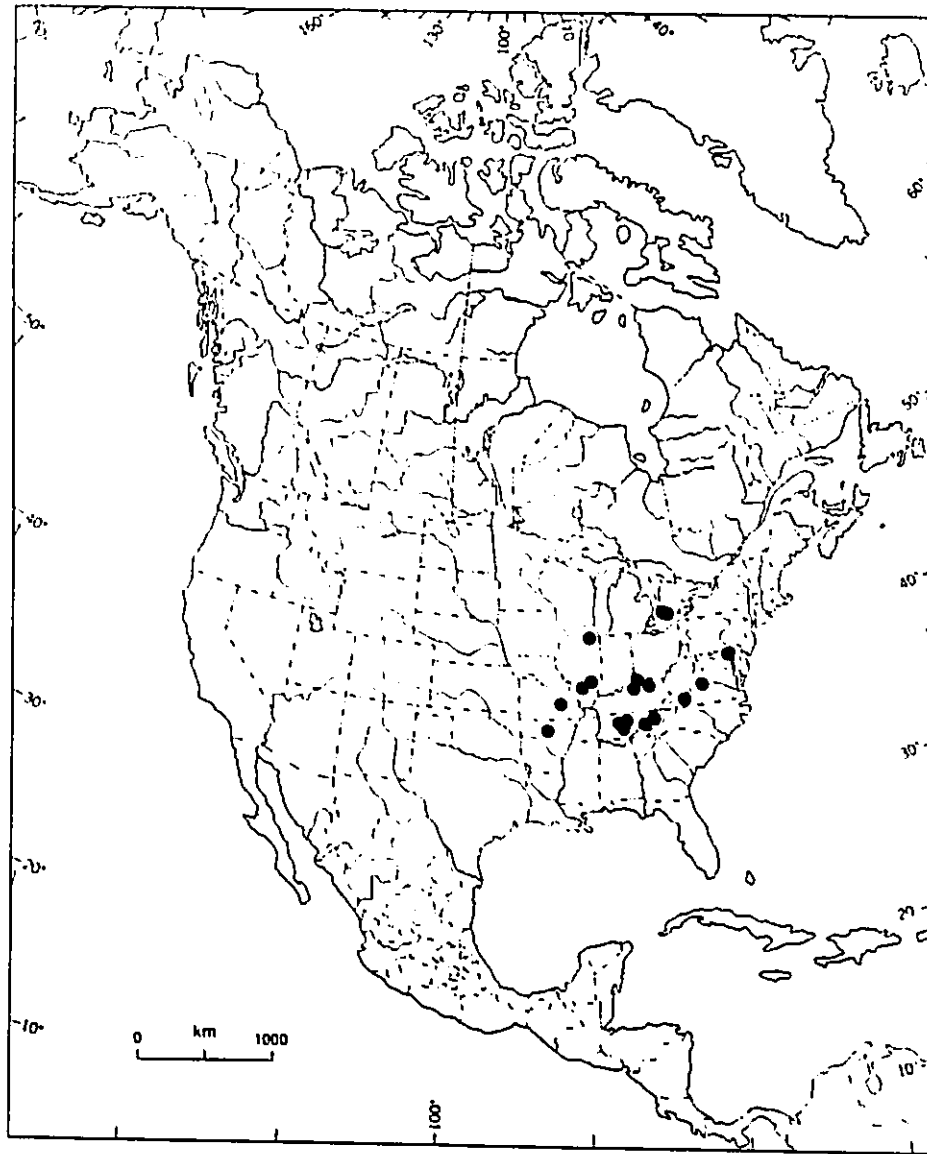


Figure 17. Distribution of *P. erectum* between 1975 and 1987.

misrepresented by "collector activity", the material of the two species came from the same herbaria so that differences in pattern are certainly a reflection of distributional changes even if differential collecting over time may obscure some details.

Having determined that *P. achoreum* originated in midwestern North America, speculation regarding factors affecting the increase in the range of *P. achoreum* and the simultaneous decrease in the range of *P. erectum* during this century can be made. *Polygonum achoreum* is common along roadsides, sidewalks, and trampled areas such as field entrances. In Nova Scotia and Alberta, plants are also found in saline marshes (Roland and Smith 1964, Moss 1969). Herbarium records also indicate that in Alberta *P. achoreum* grows in sloughs which are generally rich in salt content, and although moist in spring, can dry out in summer. Although *P. erectum* is also found along roadsides and in trampled wet fields, it is also common in naturally disturbed areas such as riverbanks, outwash areas, flood plains, and swamp and pond margins. One hypothesis is that *P. erectum*, unlike most members of the section *Polygonum*, is salt sensitive and could not survive in disturbed roadside habitats with the advent of winter road salting. Sodium concentrations and pH have been shown to be significantly higher in *P. achoreum* habitats, suggesting that *P. achoreum* is more salt tolerant than *P. erectum*. Winter road salting could therefore decrease the number of roadside habitats available for *P. erectum*.

Another variable affecting the ranges of these taxa is urbanization. It would follow that *P. achoreum*, found in dry habitats and able to withstand high sodium concentrations such as those found in saline marshes and sloughs, would with increased urbanization over this century, be able to migrate to its present range. In addition, urbanization would also raise water levels of streams and rivers, resulting in a loss of naturally disturbed outwash areas suitable for the moisture loving *P. erectum* to invade, confining it to more rural areas. It has also been suggested that the

diminishing number of small farms, which provide disturbed field edges for *P. erectum* to colonize, has contributed to its decline. More importantly, however, *P. erectum* has within the last two years been found in the northern and western parts of its range in natural and man-made disturbed areas that are not subject to winter salting, and it is possible that more locales will be found now that the taxonomy and habitat differences between the taxa have been clarified.

Determining the range and migration history of *P. erectum* has resulted in a better understanding of its present status. Known only from a few locales in southern Ontario, *P. erectum* has been given rare plant status in Ontario (Pryer and Katz 1987), and Canada (Argus and Pryer 1987). In Maine, no recent collections are known and the status of *P. erectum* to "unknown" is being urged (Sally Rooney, biological consultant, *pers. comm*). Although *P. erectum* is noted as rare in Vermont (Vermont Natural Heritage Program 1985, Special plants of Vermont. February 1985. Nature Conservancy of Vermont, Montpelier), and has been included on the threatened species list in New Hampshire (New Hampshire Natural Heritage Inventory 1985, Special plants of New Hampshire. Working list, 6 August 1985. New Hampshire Office of State Planning, Concord), the most recent collections from these states date back to 1902 and 1905, respectively. Therefore, the present status of *P. erectum* in these states needs to be re-evaluated. Since 1960, only three collections of *P. erectum* have been made from Pennsylvania. Many locations where *P. erectum* has been found prior to 1960 have since undergone rapid development, and new locations in more rural areas are being sought in an effort to evaluate its present status (Sarah Davison, Pennsylvania Nature Conservancy, *pers. comm*).

In summary, *P. achoreum* has been found to be distinct at the specific level from *P. erectum* on the basis of morphological, cytological, chemical, phenological, and geographical evidence. *Polygonum achoreum* originated in midwestern North America

from whence it migrated eastward being described from Vermont as a new species in 1917. Clarifying the taxonomy and origin of these taxa coupled with a study of available herbarium records, enables changes in the distribution of these two taxa over this century to be documented. The greater salt tolerance of *P. achoreum* coupled with the effects of urbanization, appear to be factors both contributing to the decrease in the number of suitable habitats available for *P. erectum*, and accounting for changes in the ranges of these taxa over this century.

V. TAXONOMY

Key to *P. erectum* and *P. achoreum*.

Leaves heterophyllous, bright yellow-green, elliptic; fruiting perianth deltoid shaped, the sinuses divided 3/4 the total length; achenes brown to dark brown, striate papillose with three nearly equal concave sides *P. erectum*

Leaves homophyllous, green to blue-green, obovate; fruiting perianth bottle shaped, the sinuses divided 1/3 or less the total length; achenes tan to dark tan, uniformly papillose with two broad convex and one narrow concave side *P. achoreum*

1. *Polygonum erectum* L., Sp. Pl. 363. 1753.

Type: "enata ex seminibus *D. Kalmii*". LECTOTYPE: LINN 510.26 (selected here).

Although Linnaeus described *P. erectum* from seed received from Kalm, the specimen upon which he could have based his knowledge of the species is LINN 510.26, annotated by J.E. Smith as "*erectum?*" (Savage 1945). This specimen is not annotated *P. erectum* by Linnaeus, and even if annotated, it could not be considered as the holotype because there is no way to tell if it was "the one specimen" (Art. 7.3 of the *International Code of Botanical Nomenclature* (ICBN); Voss *et al.* 1983) used to describe *P. erectum*. However, the microfiche of specimen 510.26, showing one mature achene, one flower, a few small erect branches and distinctly heterophyllous leaves, agrees with the protologue, and as it appears to have been in Linnaeus's possession prior to 1753

can be accepted as a possible nomenclatural type. It is therefore designated as a lectotype of *P. erectum*, as there has been no previous designation of a lectotype under the terms of Art. 8.1 of the ICBN. The following names, based on the variety of *P. aviculare* var. *erectum* L., although originally applied to Eurasian plants, have been misapplied to North American plants of *P. erectum*, and are frequent in North American Floras: *P. aviculare* var. *erectum* (L.) Roth., Fl. Germ. 2: 455 (1789) and *P. aviculare* var. *erectum* (L.) Ledeb., Fl. Ross. 3: 533 (1848).

Plants erect, 5.0 - 75.0 cm tall, glabrous; stems sparingly to moderately branched, ascending to erect, sometimes woody near the base, the stem internodes 5.0 - 27.0 mm long, the branch internodes 2.0 - 15.0 mm long. *Leaves* bright yellow-green, heterophyllous, elliptic, the apex broadly acute to rounded; stem leaves 13.5 - 41.0 mm long, 6.0 - 18.0 mm wide; branch leaves 7.5 - 27.0 mm long, 2.0 - 11.0 mm wide; petioles all 0.6 - 7.3 mm long; ochreae 7.0 - 17.0 mm long, hyaline-silvery, eventually becoming lacerate, with 6 - 11 veins at the base. *Inflorescence* 1 - 4 flowered. *Fruiting perianth* persistent, deltoid shaped, 2.9 - 4.1 mm long, 2.0 - 3.2 mm wide, divided 3/4 to the base; perianth segments overlapping, the free portion of the inner 0.8 - 1.7 mm wide, the free portion of the outer 1.6 - 2.9 mm wide, the margins cream-yellow to green, the apices cucullate. *Achenes* brown to dark brown, 2.0 - 3.2 mm long, 1.9 - 3.2 mm wide, striate-papillose, with three nearly equal concave sides, usually enclosed by the perianth, although occasionally the tip may protrude slightly; late season fruits not uncommon, up to 5 mm long, exserted, olivaceous, smooth. *Chromosome number* $2n = 40$. Plates 2b, 3b and 4b.

Distribution and Habitat: Presently rare in Southern Ontario, Illinois, Maryland, Missouri, West Virginia and Virginia, and infrequent in Kentucky, Tennessee, and Alabama.

Plants found in disturbed habitats such as field edges, trampled cattle pastures, stream

Plate 2. Habit of *P. achoreum* (a) and *P. erectum* (b).

a



b

1 cm

Plate 3. Fruiting perianth of *P. achoreum* (a) and *P. erectum* (b).

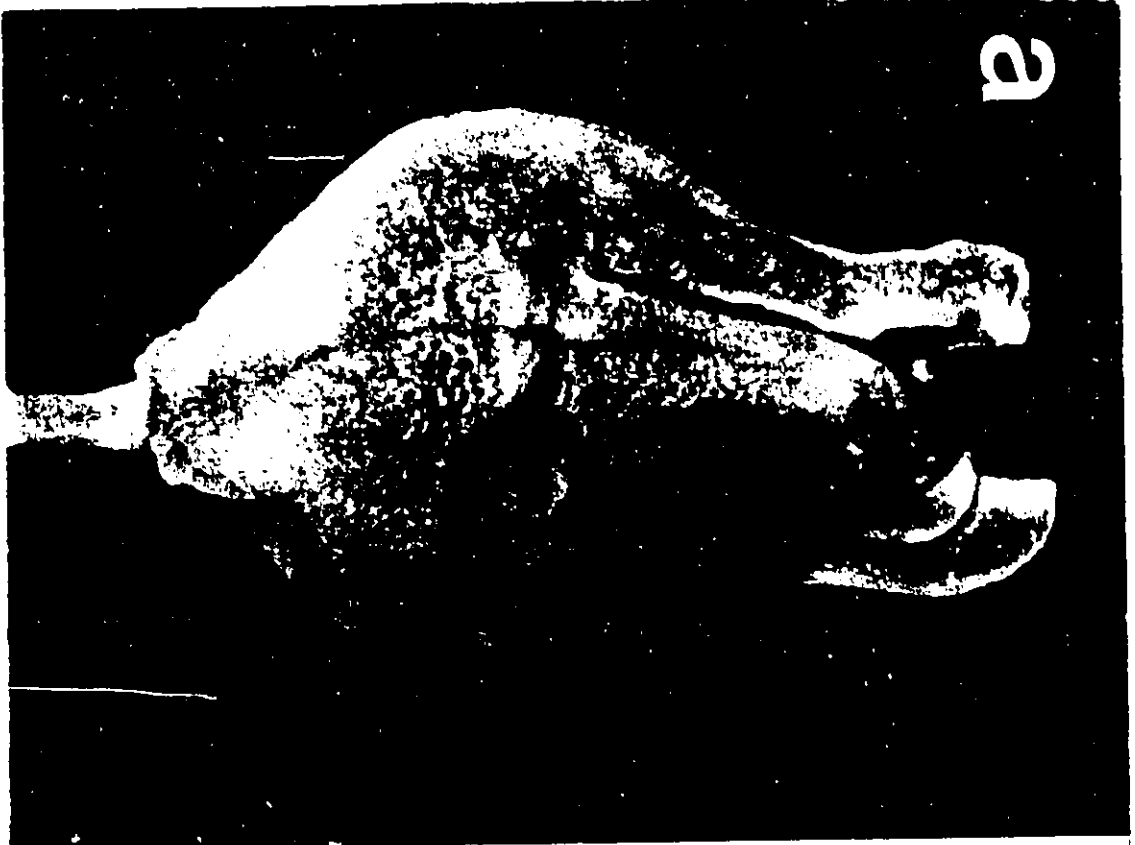
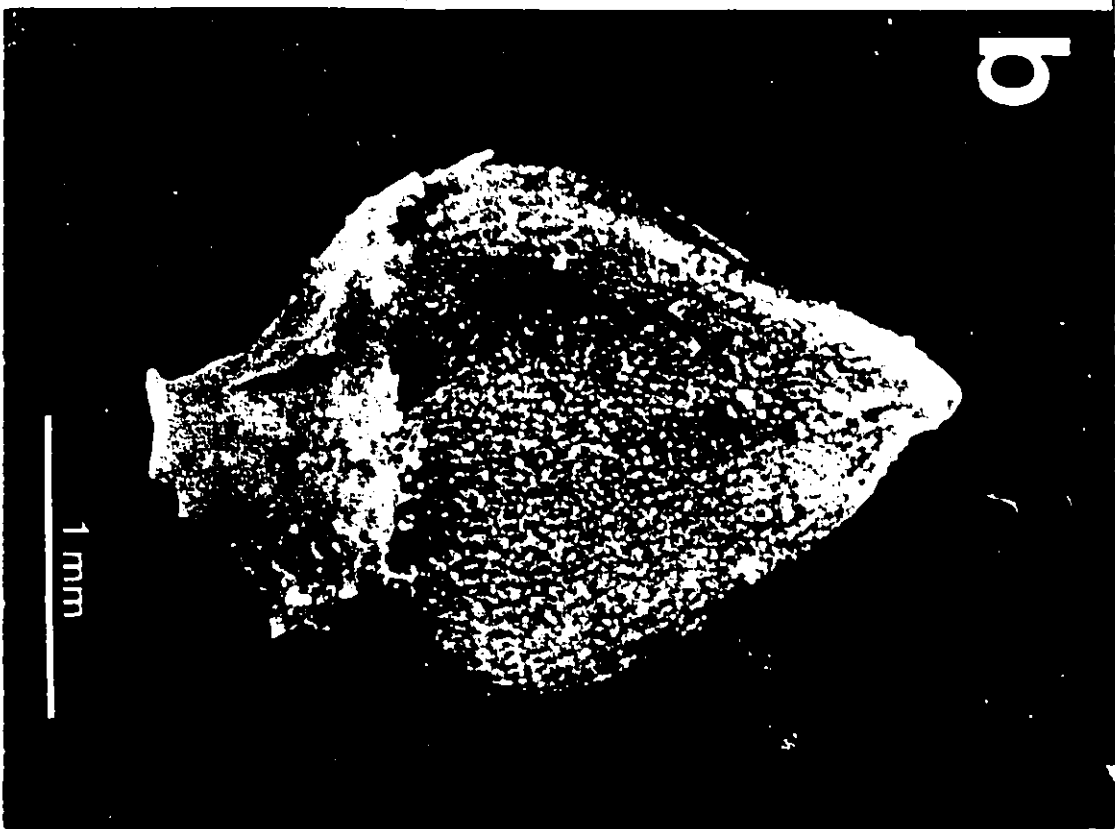
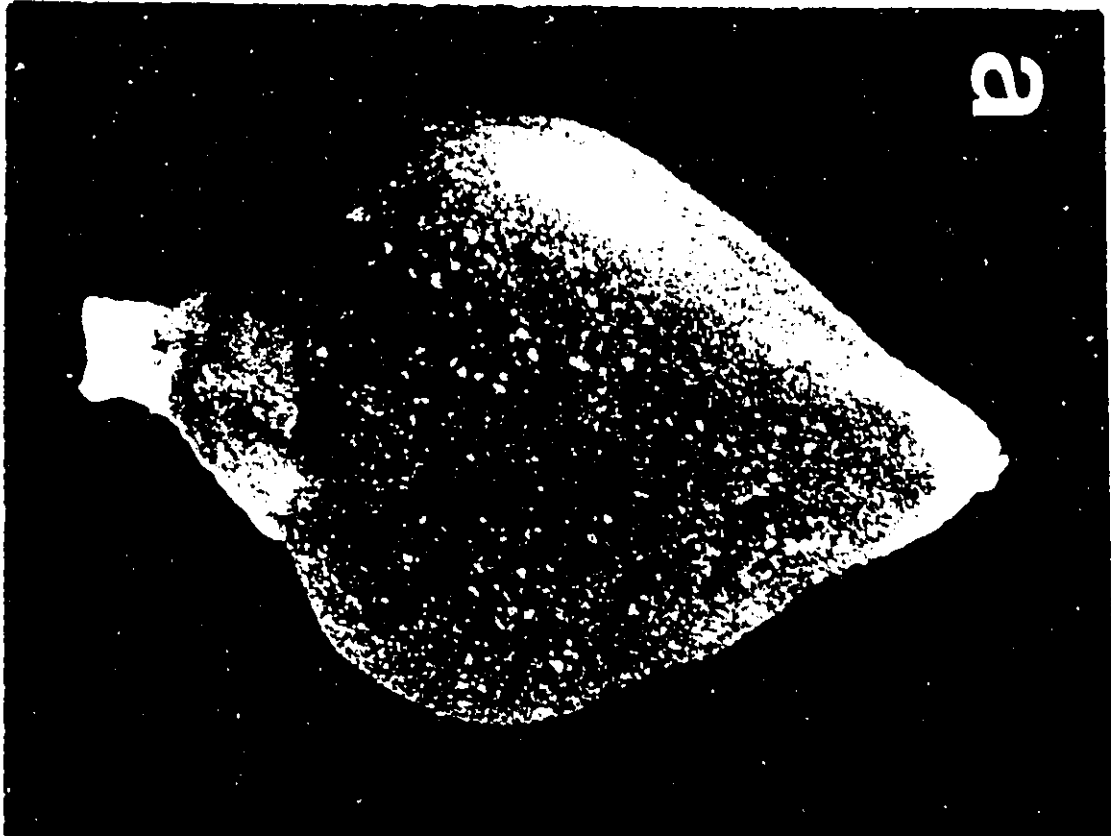


Plate 4. Achenes of *P. achoreum* (a) and *P. erectum* (b).



and river banks, floodplain outwash areas, and swamp and pond margins. Flowers from July to October.

Representative Specimens:

CANADA. ONTARIO: Elgin Co., Near St. Thomas, 20 Aug. 1951 *L.E. James* (DAO 306953); 2 Sept. 1951 (DAO 306952); 3 mi. se. of St. Thomas, 1 Sept. 1954 *L.E. James* 2448 (DAO 306955, MT); 1.5 mi. e. of St. Thomas, 17 Oct. 1956 *L.E. James* 2976 (DAO 306865). 4 Sept. 1957 *L.E. James* 3160 (DAO 306866, QFA 289718); Middlesex Co., London, 21 Oct. 1877 *T.J.W. Burgess* (DAO 306937, MT 40239, MTMG 40245); Regional municipality of Niagra, near St. Catharines, Welland Ave., 27 Aug. 1895 *W.C. McCalla* (ALTA 82268); Komoka, Wannacott's Flats, 17 July 1934 *A.A. Wood* (DAO); Peel Co., Toronto, ball grounds, 7 July 1904 *Scott* (C, CAN 43798, DAO 306867); Pelee Island, between Cooper's Road and East West Road, 28 Aug. 1986 *D.S. Katz & M.J. Oldham* 461 (DAO).

USA. ALABAMA: Colbert Co., US72 just w. of Muscle Shoals, 16 May 1973 *R. Kral* 49957 (GH, NCU 446669). Cullman Co., Cullman, 27 June 1892 *C. Mohr* (ALU 11726); Tuscaloosa Co., Tuscaloosa, 2 June 1874 *E.A. Smith* 1322 (ALU 11727).

CONNECTICUT: *C. Wright* (CM 5355); New Haven Co., New Haven, 1870's, *G.R. Kleeberger* (DS 131983); Waterbury, 3 Aug. 1910 *A.E. Blewitt* 420 (MO 935411, NEBC); Newtown, 18 Sept. 1914 *W.W. Denslow* (AC 15258); Tolland Co., Ellington, 25 Aug. 1875 *G.M. Hawes* (NY). DELAWARE: Centerville, Aug. 1866 *A. Commons* (MO 816203, NY); Willmington, 25 June 1897 *A. Commons* (NY). DISTRICT OF COLUMBIA: Washington, 18 Sept. 1899 *E.S. Steele* (C L229185, GH); Sept. 1893 *Th. Holm* (COLO 254018, S). GEORGIA: Athens, 5 July 1900 *R.M. Harper* 126 (GH, MO 3343182, NY, US 384523). ILLINOIS: (DS 132135); Chicago, 12 Aug. 1892 *W.S. Moffatt* 1342 (GH, MICH), 15978 (WIS). McDonough Co., Prairie City, 13 Sept. 1874 *H. Eggert* (CM 5335). IOWA: Ames,

27 Aug. 1896 *R. Combs & L.H. Pammel* 202 (GH, NY, US 289328); Des Moines, 15 Sept. 1894 *L.H. Pammel* (GH, MO 8343178); Grinnell, 1877 *M.E. Jones* (DS 154213, NY).

KANSAS: Atchison Co., 1896 *A.S. Hitchcock* 806 (GH, MO 3343196) Miami Co., Paola, summer 1885 *Dr. J.H. Oyster* (DS 132134). KENTUCKY: Bracken Co., Foster, route 8, ca. 1.5 mi. e. of Dam of Ohio River, 29 Aug. 1985 *D.S. Katz* 356 (DAO); Henry Co., US421, 1.3 mi. w. of Franklin-Henry Co. line, 19 July 1962 *J.L. Gentry Jr.* 495 (NCU 272306, NY). MARYLAND: Howard Co., Patuxent River, Rocky Gorge Reservoir, Brown Bridge Road Recreation Area, 19 Sept. 1981 *S.R. Hill* 10787 (MICH, NY); 26 Aug. 1985 *D.S. Katz* 339 (DAO); Montgomery Co.; Great Falls, 1 Oct. 1938 *F.J. Hermann* 9857 (MICH, NY, PH 780822); Talbot Co., Wright Mill, 1.75 mi. ne. by e. of Trappe, 4 Sept. 1951 *E.C. Earle* 4739 (GH, PH). MASSACHUSETTES: Sunderland, 1872 *C.G. Trow* (AC 44496); Berkshire Co., Williamstown, 8 Oct. 1928 *F.C. Seymour* 3355 (AC 57903); Mt. Washington, 19 Aug. 1939 *W.A. Weber* 1785 (COLO 47172); Hampden Co., Southwick, 14 Sept. 1914 *F.C. Seymour* G111 (AC 71270); Hampshire Co., Hadley, Hockhanum, 6 Aug. 1929 *F.C. Seymour* 3438 (AC 56829); Amherst, 1901 *Dr. A.E. Stone* (AC 14638), 23 Aug. 1868 *H.G. Jesup* (AC 49497), 31 Aug. 1875 *C.H.K. Sanderson* 2394 (AC 72326), 4 Sept. 1879 *W.E. Stone* (AC 14611), College Farm, 11 Sept. 1882 *C.S. Plumb* 555 (AC 14637); Worcester Co., Cambridge, near Mt. Auburn, 28 Aug. 1897 *W.P. Rich* (GH 658, 661); Mt. Auburn, 28 Aug. 1897 *E.F. Williams* (NEBC, PH 632499). MICHIGAN: Alma, 20 Aug. 1895 *C.A. Davis* (MICH, NY, WIS); Wayne Co., Detroit, Aug. 1875 *G.B. Lynn* 39795 (MICH); 1 Sept. 1875 *G.B. Lynn* 39796 (MICH). MISSOURI: Jackson Co., 8 Aug. 1893 *B.F. Bush* 324 (MO 3343193, NY); St. Louis, Sept. 1845 *G. Englemann* (NY, GH, PH 668189), Nov. 1886 *L.H. Pammel* (C L229/85). NEBRASKA: Lancaster Co., Lincoln, 1887 *H.J. Weber* (MO 3343175, US 216317). NEW JERSEY: Passaic Co., Clifton, June 1892 *Halstead's American Weeds* 187 (GH, MICH, NY, PH 587303, 598425, VPI 10559, WVA); Somerset Co., Watchung, 3 Sept. 1932 *H.N. Moldenke* 7313 (NY), 7441 (NY, MT). NEW YORK: Brooklyn, Canarsie, 7 July 1936 *J. Monachino* 83 (NY, TENN, WIS); Lake

region, western central A. Gray (GH); Dutchess Co., 2 mi. s. of Hyde Park on Rt. 9, 11 Sept. 1959 *H.E. Ahles 53015* (AC 5135); Greene Co., Greenpoint, 4 mi. s. of Catskill, 2 Sept. 1937 *H.D. House 25131* (DS, GH, NY); Rensselaer Co., Rensselaer, 11 Sept. 1939 *H.D. House 27053* (DS 277115, NY 2492); Warren Co., s. of Brayton, 30 Aug. 1942 *H.D. House 29009* (NY 2431). NORTH CAROLINA: Clay Co., 1.3 mi. s.w. of Hayesville, Jct. Sweet Water Gap Rd. and US64, 2 June 1956 *A.E. Radford & H.E. Ahles 13800* (NCU 144859, NY). OHIO: Carroll Co., Specht Marsh, 3 mi. s. of Augusta Station, 1 Sept. 1959 *L.K. Henry & W.E. Buker* (CM 153305); Coshocton Co., Coshocton, 2 Aug. 1942 *H.N. Moldenke 13470* (CM 153304); Cuyahoga Co., Berea, Aug. 1897 *G.B. Ashcroft 7587* (MO 3343181, WIS); Richland Co., 18 Sept. 1887 *E. Wilkinson* (MICH, UWO 6803); Mansfield, 11 Sept. 1896 *E. Wilkinson* (CM 308153). PENNSYLVANIA: Allegheny Co., Fern Hollow, Frick Park, 17 Sept. 1905 *O.E. Jennings* (CM 037806); Greenshaw, 27 Sept. 1914 *J. Bright* (CM 308160); Leetsdale, 25 Aug. 1946 *W.E. Buker* (CM 308158); Montrose, 16 Sept. 1905 *O.E. Jennings & S.E. Kinzer* (CM 037805); Pittsburgh, Stock Hollow, 27 Aug. 1927 *W.C. Grimm 330* (CM 308161); Rosedale, 19 Oct. 1929 *W.R. Van Dersal 399* (CM 308160, PH); 2-3 mi. w. of Elizabeth, 22 Sept. 1951 *W.E. Buker* (CM 308159); near Pittsburgh, McKee's Rocks, 15 sept. 1899 *J.A. Shafer* (CM 037811); Tilsbury, 18th Ward, July 1883 *J.A. Shafer* (CM 308164), Tilsbury, 8 Aug. 1885 *J.A. Shafer* (CM 308163); Bedford Co., 4 mi. ne. of Centerville, 3 Sept. 1939 *D. Berkheimer 1469* (CM 037803); Blair Co., Newry, 31 July 1947 *H.A. Wahl 3372* (PH); 1 mi. n. of Williamsburg, 31 July 1947 *Wahl 3415* (PH); Center Co., Bellefonte, 20 Aug. 1938 *H.A. Wahl 229* (GH, PH); Delaware Co., Darby creek, 1 mi. e. ne. of Broomall, 22 Sept. 1942 *L.C. Wheeler 5660* (AC 15307, C 15, COLO 71799, DAO 306802, DS 308986, 283727, GH, NY, MICH, MO 126206, MT, NCU 74020, NH 8789, PH, QFA 22094, S, TENN, UARK, US 1925748, WIS, WVA); Fayette Co., Cheat River at Cheat Haven, along gorge *O.E. & G.K. Jennings* (CM 037828); Greene Co., Owen's Run, 2 mi. nw. of Graysville, 29 Aug. 1951 *L.K. Henry & F.H. Beer* (CM 308156); Waynesburg, 10 Sept. 1921 *Mr. & Mrs. A.E.*

McKee and G.K. & O.E. Jennings (CM 037815); Huntingdon Co., Raystown Branch, Entriken Bridge, 8 Oct. 1947 *H.A. Wahl* 4961 (PH); Pearth Cottage, Coles, 2.5 mi. nw. of Saltillo, 24 July 1964 *D.L. Pearth* (CM 037801); Lancaster Co., Graeff's Landing, 14 Sept. 1901 *A.A. Heller* (AC 9534, GH, US 406858); Lancaster, along Conestoga River, 10 Oct. 1890 *J.K. Small* (C L229185, US 298794); vicinity of conewaga, 25 Oct. 1891 *J.K. Small* (US 298208); Lehigh Co., Allentown, 5 Oct. 1912 *H.W. Pretz* 5189 (NCU 388655, PH); Montgomery Co., 5/8 mi. s. se. of Glasgow, 27 Aug. 1944 *D. Berkheimer* 5576 (CM 037821, PH); Monroe Co., W. of Rt. 615, 2 5/8 mi. sw. of Cresco, 26 July 1951 *S.L. Glowenke* 11615 (PH, UC M006720); Philadelphia Co., W. shore of Shuylkill River, 14 Sept. 1926 *J.W. Adams* 531-A (MT, PH, UC 589327); Northhampton Co., Bethlehem, *J. Wolle* (GH); Washington Co., Mingo Creek Valley, 3 Oct. 1942 *O.E. Jennings* (CM 308157); Wheeling Creek, 5 mi. se. of Bornsville, 17 Aug. 1946 *W.E. Buker* (CM 037817); Westmoreland Co., Sept. 1881 *J.D. Block* (C L229/85); Avonmore, 10 Aug. 1902 *K.R. Holmes* (CM 037819). RHODE ISLAND: Tiverton, 27 sept. 1903 *J.M. Grennman* 1754 (GH, MO 746602). TENNESSEE: Knox Co., Knoxville, 18 Aug. 1898 *A. Ruth* 182 (MO 3343200, NY); Lake Co., Banks of the Mississippi River, 22 June 1893 *S.M. Bain* 448 (GH, NY); Montgomery Co., Flood plain of Red River, 20 Sept. 1941 *R.E. Shanks* 835 (TENN, WIS); Sumner Co., Butler Bridge RR shoulder crossing se. side, 30 Aug. 1985 *D.S. Katz* 360 (DAO); Sevier Co., Sugar Loaf Road, 31 Aug. 1985 *D.S. Katz* 363 (DAO); Dupont, n. slope of Sugarloaf Mtn., ca. 7 mi. s. of Sevierville, 18 Aug. 1986 *R.D. Thomas, S. Thomas & J. Berry* 97883 (NLU). VERMONT: Bennington Co., Bennington, Mill St., 5 Sept. 1897 *W.W. Eggleston* (AC 83407). VIRGINIA: Culpepper Co., pasture on US211 and Rappahannock River, 12 Sept. 1965 *H.E. Ahles & F. James* 61469 (AC 53005, NCU 263389); Fauquier Co., Beverly Mill, 13 Sept. 1942 *H.A. Allard* 10453 (CM 308154, GH, MO 1262285, NH 2504, VPI); w. slope of Bull Run Mtn., 4 Oct. 1942 *H.A. Allard* 10499 (CM 153303, VPI 10175); Beverly Mill, western slope, 12 Sept. 1943 *H.A. Allard* 11036 (GH, WVA); Giles Co., Bluff along New River, 0.75 mi. se. of Pembroke, 11

Sept. 1982 *T.F. Wieboldt* 4535 (CM 286798); Greene Co., 0.25 mi. e. of Quinque, 4 Aug. 1951 J.R. Harlow 1414\ (DAO 306864, VPI 35315); Scott Co., Lowland along N. Fork Holston River, margin of St. Rt. 689 just ne. of hwy. 58 bridge, 0.5 mi. e. of Hiltons, 23 Sept. 1985 *T.F. Wieboldt s.n.* (VPI). Sussex Co., Waverly, 26 Aug. 1940 *M.L. Fernald & B. Long* 12636 (GH, PH). WEST VIRGINIA: Whirliug, 22 Sept. 1878 *G. Guttenburg* (CM 308155); Ohio Co., Stratford Hill, 25 Sept. 1937 *R. West* 846 (DS 398338, WVA); Upshur Co., ca. 4 mi. s. of Buckhannon, between Hickory Flat Run and Buckhannon River, 29 Sept 1962 *G.B. Roszbach* 4186 (AC, WVA); Wetzel Co., Littleton, roadside at mouth of Wolf Run, 24 Aug. 1931 *O. Haught* 875 (DS 283727);

Miscellaneous. Goat Island, 12 Sept. 1890 *N.T. Kidder* (GH). (Additional records available upon request.)

2. *Polygonum achoreum* Blake, *Rhodora*: 19: 232. 1917.

Type: "VERMONT: in paths, Queen City Park, South Burlington, 13 Aug. 1911, *Blake* 2766". (HOLOTYPE GH, NYI; ISOTYPE SI).

Plants erect, 5.0 - 50.0 cm tall, glabrous; stems moderately to heavily branched, ascending, sometimes woody near the base, the stem internodes 1.3 - 32.6 mm long, the branch internodes 2.0 - 19.6 mm long. *Leaves* green to blue-green, homophyllous, 7.5 - 33.0 mm long, 3.5 - 17.0 mm wide, obovate, the apex rounded to obtuse; petioles 0.4 - 4.0 mm long; ochreae 4.0 - 11.0 mm long, becoming reddish-brown and lacerate, with 2 - 6 veins at the base. *Inflorescence* 1 - 4 flowered. *Fruiting perianth* persistent, bottle shaped, 3.2 - 4.8 mm long, 2.1 - 3.5 mm wide, divided 1/3 or less to the base; perianth segments usually overlapping, the free portion of the inner 0.4 - 1.1 mm wide, the free portion of the outer 0.8 - 2.1 mm wide, the margins cream to green, the apices

cucullate. *Achenes* tan to dark tan, (yellow-green when immature), 2.4 - 3.3 mm long, 1.6 - 2.4 mm wide, uniformly papillose, with two broad convex and one narrow concave side, included in the perianth; late season fruits common, up to 5 mm long, exserted, olivaceous, smooth. *Chromosome number* $2n = 40$ and $2n = 60$. Plates 2a, 3a and 4a.

Distribution and Habitat: Common in disturbed areas such as roadsides, sidewalks, building sites, trampled paths, field entrances, from the Northwest Territories, south to Colorado, and from Alberta in the west to Newfoundland in the east.

Representative Specimens:

CANADA: NORTHWEST TERRITORIES: Mackenzie hwy., 22 mi. n. of Manning; 57° 20'N 117° 48'W, 18 Aug. 1969 J. Nagy 8 (AC). ALBERTA: Edmonton, corner of 102 Avenue and 105 Street, 4 Oct. 1986 S.R. Downie and D.S. Katz 750 (DAO); Peace River District, Key River, 25 Aug. 1946 H. Groh 2919 (DAO 306897). SASKATCHEWAN: District de Rosetown, Demaine, ca. 12 mi. au sud-est, ferme LeFort, 28 July 1956 B. Boivin, F.L. LeFort et J.G. Vaillancourt 11600 (DAO 146452, UBC 155407). MANITOBA: Churchill District, The Pas Indian Reserve, 27 July 1955 W. Krivda 1596 (DAO 146446). ONTARIO: Carleton Co., Ottawa, Kent Street between Slater and Albert, 19 Aug. 1985 D.S. Katz 335 (DAO); Sudbury district, 100 km south of Timmins, off hwy. 144 near Arctic - Atlantic watershed, 20 Aug. 1985 L.L. Consaul & L. Goodfellow 718. QUÉBEC: Comté Île de Montréal, Ste. Anne-de-Bellevue, Macdonald College Campus entrance road near hockey arena, 6 Oct. 1985, D.S.Katz 368 (DAO); Comté Montmorency No. 2, St. François, 3959 Avenue Royale, 31 Aug. 1986 D.S. Katz 479 (DAO), The Simmon's driveway, 31 Aug. 1986 D.S. Katz 489; St. Jean, 1056 Avenue Royale, 31 Aug. 1986 D.S. Katz 480 (DAO), 3188 Avenue Royale, 31 Aug. 1986 D.S. Katz 481 (DAO); Ste. Pétronille, opposite 2964 Avenue Royale, 31 Aug. 1986 D.S. Katz 488 (DAO). NEW BRUNSWICK:

Carleton Co., Woodstock, 28 July 1945 *W.G. Dore & E. Gorham* 45.895 (DAO 306974, QFA 251464).

USA. IDAHO: Bonneville Co., 3 mi. s. of Ashton, 19 July 1945 *J.H. Christ & W.W. Ward* 14980 (NY). MONTANA: Fergus Co., Lewiston, Main Street, 19 July 1979 *W.A. Weber* 15475 (COLO 330334, 330335). SOUTH DAKOTA: Mellette, 7 July 1940 *J.F. Brenckle* 37-01 (US 1826755, 1826756), 1 Aug. 1940 *J.F. Brenckle* 38-62 (GH, DAO 306869). MINNESOTA: Clearwater Co., Itasca State Park Biological Station, *J.W. Thieret* 33614 (LAFF 51119). MICHIGAN: Chippewa Co., ca. 11 mi. by road w. of Paradise, near Lower Falls of Tahquamenon River, 17 July 1952 *R. McVaugh* 12761 (MICH). VERMONT: Washington Co., Cabot, 1.7 km w. of Caledonia Co. line on US2, roadside, 2 July 1983 *D.E. Boufford & E.W. Wood* 23152 (WIS). MAINE: Aroostock Co., Presque Isle, 7 mi. s. of Caribou, 15 Sept. 1986 *D.S. Katz, S. Rooney, M. Rasmussen* 493 (DAO). (Additional records available upon request.)

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Appendix 1. Vegetative and floral-achene OTU by character matrices.

A. Vegetative OTU by character matrix

AAA1	19.5	10.0	9.0	2.0	19.0	10.0	10.0	1.7	14.0	8.0	6.0	1.3	8.7
	2.0	6.0	4.0										
AAA2	14.5	8.0	7.5	0.9	15.0	10.0	8.0	1.3	9.0	5.0	5.0	0.6	8.3
	2.0	7.0	4.0										
AAA3	19.0	11.0	9.0	1.7	19.0	10.0	10.0	1.6	12.0	7.0	6.5	0.6	7.3
	4.6	7.0	4.0										
AAB1	17.0	10.0	7.5	1.3	16.5	10.0	9.0	1.3	13.0	7.0	5.5	0.6	9.3
	5.3	7.0	4.0										
AAB2	16.0	10.0	7.0	1.3	14.0	8.0	7.0	1.1	11.0	7.0	5.0	0.6	9.3
	5.3	6.0	4.0										
AAC1	20.0	11.0	8.5	2.0	20.0	11.0	10.0	2.0	14.0	13.0	7.0	1.3	9.0
	5.7	8.0	4.0										
ABA1	16.0	9.0	8.0	0.9	14.5	8.0	7.0	0.6	11.0	5.0	5.5	0.5	9.0
	4.0	8.0	4.0										
ABB1	12.3	7.0	6.4	0.9	10.5	6.0	5.5	0.5	8.0	4.0	4.0	0.4	5.8
	2.7	6.0	3.0										
ACA1	16.0	10.0	7.5	1.3	17.0	10.0	8.0	1.3	14.0	8.0	6.5	1.6	9.3
	9.0	7.0	5.0										
ACA2	13.5	9.0	7.0	2.0	15.0	10.0	8.5	2.6	12.5	9.0	7.0	1.3	10.3
	8.0	7.0	6.0										
ACB1	16.0	10.0	7.5	0.9	14.5	8.0	7.0	1.1	11.0	6.0	5.5	1.1	9.0
	6.3	7.0	6.0										
ACB2	16.0	10.0	6.5	2.0	15.0	10.0	7.5	0.6	11.5	7.0	5.5	1.7	8.6
	4.3	7.0	5.0										
ACC1	11.5	7.0	5.5	1.1	11.0	5.0	5.0	0.8	12.0	7.0	5.5	0.6	7.3
	3.3	6.0	6.0										
ACC2	15.0	9.0	6.5	0.9	15.0	10.0	6.5	1.3	10.0	6.0	5.5	1.1	8.0
	4.3	6.0	5.0										
ADA1	16.5	10.0	8.0	2.0	17.0	11.0	8.0	0.9	12.5	7.0	5.5	0.6	9.0
	6.0	7.0	4.0										
ADB1	18.0	10.0	8.0	1.4	17.0	10.0	8.0	1.3	13.5	8.0	6.5	1.5	12.0
	9.3	7.0	5.0										
ADB2	16.0	10.0	8.0	1.7	16.0	9.0	7.0	1.3	12.5	7.0	6.0	0.9	8.1
	8.0	7.0	4.0										
AEA1	24.0	15.0	6.0	1.5	22.0	11.0	6.0	1.3	23.0	14.0	6.0	1.3	9.7
	6.7	8.0	4.0										
AEA2	17.0	11.0	8.0	2.0	17.5	10.0	7.5	2.0	12.5	7.0	6.5	1.3	9.3
	4.6	9.0	4.0										
AEB1	16.0	9.0	9.0	0.8	16.0	10.0	8.5	1.3	13.5	8.0	6.5	0.8	8.0
	8.3	7.0	4.0										
AEC1	18.5	10.0	8.5	2.4	15.5	10.0	7.5	0.9	12.5	7.0	5.5	0.6	10.3
	7.6	8.0	6.0										
AFA1	20.0	10.0	11.0	2.0	18.5	10.0	10.0	1.3	16.0	10.0	7.0	2.0	13.0
	12.6	7.0	4.0										
AFA2	17.0	10.0	7.5	1.6	17.5	10.0	8.5	1.7	14.0	8.0	6.0	1.6	13.6
	7.3	8.0	4.0										
AFB1	18.5	11.0	8.0	3.3	18.0	11.0	7.5	1.3	16.0	10.0	7.0	1.3	16.3

	14.0	7.0	4.0										
AFB2	16.5	10.0	7.5	1.3	17.0	10.0	7.5	1.3	13.5	8.0	6.5	0.9	13.6
	4.6	7.0	4.0										
AFC1	24.5	15.0	11.5	2.9	27.0	14.0	13.0	2.7	22.0	10.0	10.5	2.0	26.0
	19.3	9.0	4.0										
AFC2	25.0	10.0	13.0	1.6	21.5	12.0	10.0	2.9	18.0	11.0	9.5	1.6	30.0
	8.7	8.0	4.0										
AFD1	14.0	8.0	7.0	1.3	13.5	7.0	7.0	1.3	10.5	6.0	5.0	0.6	6.0
	6.3	6.0	4.0										
AFD2	10.5	6.0	5.5	0.6	11.0	6.0	5.5	0.6	9.5	5.0	4.5	0.6	5.6
	6.0	7.0	2.0										
AGA1	20.5	12.0	9.5	2.3	19.0	11.0	8.5	1.6	12.0	7.0	6.0	2.0	9.6
	7.3	6.0	4.0										
AGA2	22.0	12.0	9.5	2.7	20.5	12.0	9.5	2.3	14.5	8.0	6.5	1.3	9.0
	6.6	7.0	4.0										
AGB1	18.5	9.5	10.0	2.0	17.0	10.0	9.5	1.1	14.5	8.0	7.0	0.6	22.0
	19.6	7.0	4.0										
AGB2	13.5	7.0	7.5	0.9	14.0	8.0	7.5	0.8	10.5	5.0	5.5	0.6	9.6
	9.0	6.0	4.0										
AGC1	17.5	10.0	9.0	1.3	18.5	9.0	9.0	1.7	12.5	6.0	7.0	0.5	5.3
	6.6	8.0	4.0										
AGD1	17.5	10.0	8.5	1.5	15.5	8.0	7.5	1.1	12.0	6.0	5.0	0.9	8.0
	6.0	7.0	4.0										
AGD2	18.0	11.0	9.0	1.3	18.5	10.0	9.5	1.6	12.5	7.0	6.0	0.9	13.3
	7.3	6.0	4.0										
AGE1	19.5	11.0	10.5	2.3	19.5	12.0	10.5	2.3	13.0	8.0	6.5	2.0	13.3
	9.0	8.0	4.0										
AGE2	18.5	10.0	8.5	2.0	19.0	11.0	9.5	2.3	12.5	7.0	6.5	1.3	9.3
	7.3	7.0	4.0										
AHA1	16.0	10.0	7.5	1.3	17.0	10.0	8.5	0.9	9.0	5.0	4.5	0.6	9.1
	6.5	4.0	4.0										
AHB1	13.5	7.5	7.5	1.3	12.0	8.0	6.0	1.0	14.5	8.0	7.5	1.2	7.3
	3.3	8.0	4.0										
AIA1	19.0	10.0	9.0	1.6	17.0	11.0	8.5	0.9	14.0	7.5	6.5	1.3	14.6
	10.3	8.0	4.0										
AIB1	17.5	11.0	8.5	0.9	17.5	9.0	8.5	0.8	11.0	6.0	5.0	0.6	5.0
	4.0	8.0	4.0										
AJA1	16.0	13.0	7.0	1.3	16.0	8.0	7.5	1.3	12.0	6.0	5.5	0.9	5.6
	5.0	7.0	4.0										
AJA2	15.0	8.0	7.0	1.5	14.0	8.0	7.0	1.6	10.5	6.0	5.5	0.9	5.0
	4.0	7.0	4.0										
AJB1	17.0	9.0	7.5	1.3	16.5	10.0	8.0	1.3	12.0	6.0	5.5	1.3	7.8
	7.5	8.0	4.0										
AJC1	13.0	8.0	7.0	1.3	13.5	7.0	7.0	0.8	10.0	5.0	5.0	0.9	7.5
	3.6	7.0	4.0										
AJC2	16.0	9.0	8.0	1.6	15.5	10.0	7.5	0.9	12.0	7.0	5.5	0.6	8.6
	4.7	8.0	4.0										
AKA1	14.0	8.0	7.5	0.9	15.0	8.0	7.5	1.2	13.0	8.0	7.5	1.1	11.0
	4.5	6.0	4.0										
AKB1	13.0	8.0	7.5	0.9	13.0	8.0	7.0	0.8	9.0	5.0	5.0	0.6	8.0
	2.5	6.5	4.0										
ALA1	19.0	10.0	9.0	1.3	20.0	10.0	10.0	2.0	13.0	8.0	8.5	1.3	17.0
	8.0	9.6	4.0										
ALB1	23.0	12.0	11.0	2.0	23.0	13.0	10.5	2.0	10.0	6.0	5.5	0.9	22.0

	4.0	11.0	4.0										
AMA1	13.5	8.0	5.0	1.6	15.5	9.0	9.0	1.3	12.0	7.0	5.0	0.8	10.0
	4.0	8.5	4.0										
AMB2	17.0	9.0	7.0	0.9	16.0	10.0	8.0	1.6	11.5	6.5	5.0	0.6	10.5
	4.5	6.5	4.0										
ANA1	18.0	11.0	7.0	1.3	17.0	9.0	6.5	0.9	12.0	7.0	4.5	1.1	14.5
	7.3	6.5	4.0										
ANB1	21.0	12.0	8.0	1.3	18.0	8.0	7.5	0.6	14.0	7.0	5.5	0.8	14.0
	8.0	7.3	4.0										
AOA1	13.5	9.0	6.0	1.3	14.0	8.0	7.0	1.2	7.5	4.0	3.5	1.0	1.3
	4.5	5.0	4.0										
AOB1	17.0	8.0	7.5	1.3	16.5	10.0	7.0	1.3	13.0	7.0	6.0	1.1	6.5
	6.0	6.5	4.0										
APA1	15.0	10.0	5.0	1.5	13.5	10.0	6.5	1.3	11.5	8.0	4.5	1.3	14.0
	5.3	6.7	4.0										
APB1	14.0	9.0	6.0	1.6	15.0	10.0	7.0	1.3	11.0	7.0	5.0	0.6	10.6
	4.6	6.7	4.0										
AQA1	33.0	22.0	17.0	4.0	32.0	23.0	11.0	3.3	21.0	12.0	8.0	2.1	32.6
	15.0	10.0	4.0										
AQB1	26.0	15.0	8.0	2.1	25.0	15.0	8.0	2.0	21.0	15.0	6.0	2.0	12.0
	8.3	10.0	4.0										
ARA1	19.0	14.0	8.5	2.0	20.0	14.0	9.0	1.7	17.5	10.0	7.5	1.1	10.0
	10.6	8.0	4.0										
ARB1	16.5	10.0	7.0	1.1	15.0	10.0	7.5	0.6	12.0	8.0	6.0	0.6	12.6
	8.0	6.6	4.0										
ASA1	19.5	11.0	9.5	1.3	16.0	9.0	8.5	0.6	12.0	7.0	6.0	0.6	8.6
	6.6	10.0	6.0										
ASB1	18.0	12.0	7.0	2.0	17.0	11.0	7.0	1.6	12.5	7.0	6.5	0.6	8.6
	5.6	6.0	4.0										
ATA1	12.0	8.0	6.5	0.9	11.5	8.0	6.5	1.1	9.5	5.0	4.5	0.9	8.0
	4.6	4.7	4.0										
ATB1	17.5	10.0	9.5	1.3	17.0	11.0	8.5	1.6	13.0	8.0	6.5	0.9	13.3
	10.3	6.6	4.0										
AUA1	26.5	20.0	12.5	2.0	27.5	20.0	10.5	2.6	15.0	8.0	6.0	1.3	20.6
	16.3	8.0	4.0										
AUB1	20.0	12.0	8.0	0.9	20.0	12.0	7.5	1.3	13.5	9.0	5.0	1.5	15.3
	6.7	6.7	4.0										
AUC1	25.0	15.0	12.0	2.0	24.5	15.0	10.0	1.3	15.5	10.0	6.0	2.0	20.6
	14.6	8.0	6.0										
AUD1	23.0	17.0	8.5	2.4	23.0	17.0	8.5	2.0	15.0	10.0	6.0	1.6	19.3
	11.00	8.0	6.0										
AVA1	20.0	14.0	7.5	2.0	18.5	13.0	8.0	1.3	10.0	7.0	4.0	0.5	11.6
	3.0	8.0	4.0										
AVB1	20.0	14.0	7.5	2.0	18.5	13.0	8.0	1.3	10.0	7.0	4.0	0.5	11.6
	3.0	8.0	4.0										
AVC1	20.0	13.0	8.0	2.0	20.0	14.0	8.0	2.0	12.5	8.5	5.0	1.1	10.3
	4.3	8.0	6.0										
BAA1	18.0	11.0	5.0	2.0	18.0	10.0	5.5	2.0	12.5	6.5	3.5	0.6	14.0
	6.4	6.0	4.0										
BAB1	18.0	11.0	5.0	2.0	17.0	10.0	6.0	1.6	11.0	7.0	3.5	0.9	11.5
	5.5	6.5	4.0										
BAC1	16.0	9.0	5.0	1.3	17.0	10.0	4.5	1.9	12.0	5.0	3.0	0.6	12.6
	4.4	6.0	4.0										
BBA1	17.5	11.0	6.5	1.2	17.0	11.0	7.5	2.6	10.0	6.0	3.0	0.9	9.5

	3.3	7.0	4.0										
BBB1	16.5	10.0	5.5	2.0	16.5	10.0	5.0	1.7	10.5	6.0	4.5	0.9	8.6
	5.0	6.0	4.0										
BBC1	13.5	8.0	4.5	1.3	14.0	9.0	5.0	1.5	13.5	8.0	4.0	1.1	9.3
	3.0	6.0	4.0										
BBD1	12.0	8.0	4.5	1.5	11.0	5.0	4.0	1.2	10.5	7.0	3.5	0.8	6.3
	3.0	7.0	6.0										
BCA1	17.0	8.0	5.0	0.8	17.0	10.0	4.5	1.3	9.5	5.0	3.0	0.5	16.0
	7.0	6.0	4.0										
BCB1	21.0	10.0	7.0	1.3	21.5	13.0	6.5	1.7	13.5	7.0	3.5	0.9	15.3
	5.7	7.0	6.0										
BDA1	17.0	9.0	6.0	1.3	15.0	9.0	5.5	1.2	14.0	8.0	5.0	1.1	13.0
	5.7	6.0	6.0										
BDB1	15.0	9.0	5.5	1.1	15.0	9.0	5.0	1.2	11.5	7.0	4.0	0.8	9.5
	3.5	5.0	4.0										
BDC1	15.0	7.0	6.5	0.8	14.5	8.0	5.5	1.1	9.0	5.0	3.0	0.9	7.0
	2.0	5.0	4.0										
BDD1	17.0	10.0	5.0	1.3	14.5	8.0	4.0	1.3	9.0	5.0	2.0	0.6	14.0
	5.3	6.0	6.0										
BDE1	18.5	10.0	6.5	1.3	17.5	10.0	6.0	1.1	14.5	7.0	4.5	0.8	12.0
	4.6	7.0	6.0										
BEA1	21.0	13.0	4.0	1.6	17.5	10.0	3.5	1.1	9.0	5.0	2.5	0.6	17.3
	3.0	7.3	4.0										
BEB1	23.5	15.0	5.5	3.3	23.0	15.0	5.0	2.3	13.0	8.0	2.5	1.3	15.0
	6.3	6.7	4.0										
BEC1	22.5	16.0	6.0	1.7	23.0	15.0	6.0	2.0	13.0	7.0	3.5	0.9	19.3
	3.3	7.3	4.0										
BFA1	25.5	11.0	6.5	2.7	25.0	14.0	7.0	2.0	15.0	7.0	5.0	0.9	21.3
	6.0	7.3	4.0										
BFB1	23.0	14.0	5.0	2.0	23.5	17.0	5.5	2.0	13.0	7.0	4.5	1.3	17.0
	5.0	6.6	4.0										
BGA1	17.0	8.0	5.5	1.7	15.0	10.0	5.0	1.8	11.5	5.0	3.0	0.9	12.6
	3.5	6.7	6.0										
BGB1	15.5	10.0	4.5	1.3	15.0	7.0	5.0	0.9	10.0	5.0	3.5	0.8	2.5
	3.0	5.5	4.0										
BGC1	13.0	7.0	3.5	0.9	13.0	7.0	3.5	0.9	9.0	5.0	2.5	0.6	9.3
	3.0	5.5	4.0										
BHA1	21.0	10.0	4.5	2.0	16.0	7.0	3.5	1.3	8.0	4.0	2.5	0.6	12.5
	3.0	7.0	4.0										
BHB1	17.0	10.0	3.0	1.3	14.0	7.0	3.0	1.3	6.0	3.0	2.0	0.5	9.0
	2.5	5.5	4.0										
BIA1	20.0	12.0	4.5	1.7	22.0	12.0	4.5	1.7	11.0	6.5	3.0	0.6	14.0
	2.5	8.0	4.0										
BIB1	18.0	9.0	4.5	1.3	17.0	9.0	4.5	1.3	8.5	4.0	2.0	0.6	11.6
	2.6	6.0	6.0										
BJA1	17.5	8.0	3.0	2.0	10.0	6.0	2.5	1.3	8.0	5.0	3.0	1.3	9.6
	7.0	9.4	6.0										
BJB1	16.0	10.0	4.5	2.0	20.5	9.0	4.5	1.3	10.0	5.0	3.0	0.6	12.6
	6.0	7.3	4.0										
BJC1	14.0	8.0	3.5	2.0	13.0	8.0	3.0	0.9	7.0	4.0	2.0	1.2	9.3
	4.6	6.6	4.0										
EAA1	23.5	13.0	8.5	1.6	30.0	16.0	10.0	2.3	9.0	5.0	3.5	0.6	8.0
	4.0	7.0	6.0										
EAA2	30.0	16.0	10.0	2.3	28.0	16.0	10.5	2.0	10.0	7.0	4.0	0.6	10.0

	4.0	8.0	8.0										
EAB1	31.0	20.0	10.0	1.6	32.0	16.0	12.0	2.0	11.0	7.0	4.5	0.6	12.0
	3.5	8.0	9.0										
EAB2	32.0	16.0	12.0	2.0	31.5	18.0	12.0	2.0	10.0	6.0	4.5	0.6	10.0
	3.5	7.0	8.0										
EAC1	38.5	25.0	13.5	1.7	38.0	20.0	14.0	2.0	20.0	17.0	7.5	0.6	15.0
	5.5	15.0	9.0										
EAC2	38.0	20.0	14.0	2.0	38.0	20.0	15.0	2.0	22.0	13.0	8.5	0.8	9.5
	6.0	10.0	8.0										
EBA1	34.0	25.0	13.0	3.3	35.0	25.0	13.0	3.3	24.0	15.0	8.0	2.0	15.6
	11.0	17.0	9.0										
EBA2	35.0	25.0	13.0	3.3	35.0	22.0	14.0	2.5	27.0	15.0	9.0	2.0	15.6
	12.3	17.0	9.0										
EBB1	38.0	20.0	14.0	2.0	36.0	15.0	15.0	3.3	21.5	12.0	7.5	1.5	9.2
	6.2	8.0	7.0										
EBB2	36.0	15.0	15.0	3.3	34.0	20.0	8.0	2.0	18.0	10.0	7.5	1.0	11.0
	5.8	10.0	7.0										
EBC1	40.0	27.0	16.0	2.5	36.0	20.0	17.5	2.0	21.0	13.0	8.5	2.0	14.5
	5.0	13.0	9.0										
EBC2	37.0	21.0	17.0	2.0	32.5	19.0	16.0	2.0	22.5	16.0	9.5	1.5	11.5
	6.8	12.0	10.0										
EBD1	40.0	25.0	18.0	1.5	38.0	24.0	15.0	2.5	20.0	16.0	7.5	2.0	9.8
	4.0	12.0	9.0										
EBD2	36.5	25.0	15.0	2.0	33.5	20.0	13.5	1.0	12.5	8.0	5.5	1.0	8.0
	5.0	10.0	9.0										
EBE1	24.0	15.0	9.0	1.5	26.0	15.0	10.0	1.0	14.0	8.0	5.5	1.5	9.0
	6.0	11.0	8.0										
EBE2	26.5	16.0	12.0	1.5	22.0	10.0	11.5	1.5	14.0	8.0	6.0	1.0	8.0
	4.0	10.0	9.0										
EBF1	35.0	20.0	15.0	2.5	34.0	20.0	15.5	1.5	23.5	14.0	10.0	1.5	21.0
	10.0	11.0	9.0										
EBF2	33.0	17.0	16.0	1.5	34.0	20.0	15.0	1.5	24.5	12.0	11.0	1.5	18.5
	12.8	11.0	9.0										
ECA1	34.5	20.0	12.5	2.0	25.0	14.0	9.0	1.3	15.0	9.0	6.5	1.0	10.3
	10.0	9.0	9.0										
ECA2	34.5	20.0	11.5	2.0	31.5	20.0	11.5	1.5	16.5	10.0	6.5	1.0	16.0
	7.0	10.0	9.0										
ECB1	22.0	10.0	9.5	1.3	21.5	10.0	10.5	1.3	12.0	9.0	5.5	0.6	14.6
	11.0	10.0	10.0										
ECB2	21.5	10.0	10.5	1.3	21.5	9.0	10.5	1.2	18.0	11.0	6.5	0.9	17.6
	9.0	9.0	9.0										
ECC1	24.5	15.0	8.5	1.6	25.0	15.0	8.5	1.1	12.5	8.0	5.5	0.8	15.0
	3.5	8.0	9.0										
ECC2	24.5	15.0	8.5	1.6	25.0	15.0	8.5	1.1	12.5	8.0	5.5	0.8	15.0
	3.5	8.0	9.0										
ECD1	22.5	13.0	8.5	1.3	28.0	16.0	11.0	1.3	20.0	10.0	7.0	0.9	13.5
	8.0	9.0	8.0										
ECE1	26.5	14.0	9.0	2.0	13.5	9.0	6.0	1.0	26.0	15.0	9.0	0.9	16.3
	3.6	8.0	7.0										
ECE2	33.5	21.0	12.0	1.2	31.0	17.0	11.0	1.3	20.0	11.0	7.0	1.0	20.0
	10.6	8.0	11.0										
ECF1	28.0	20.0	12.0	1.3	25.0	14.0	12.5	1.3	19.0	10.0	8.5	1.2	16.0
	13.0	7.0	9.0										
EDA1	25.0	12.0	8.0	2.6	23.0	17.0	8.5	2.0	11.0	7.0	4.0	0.6	14.0

	2.0	8.0	7.0										
EDA2	23.0	17.0	8.5	2.0	27.5	16.0	10.0	2.6	11.0	7.0	4.0	0.8	17.0
	2.0	8.0	8.0										
EDB1	35.0	22.0	9.5	2.6	28.0	17.0	7.5	3.3	8.5	5.0	2.0	0.6	10.6
	2.0	7.0	6.0										
EDB2	28.0	17.0	7.5	3.3	29.0	17.0	8.0	2.6	7.5	5.0	2.5	0.9	8.0
	3.0	8.0	6.0										
EEA1	27.5	15.0	8.5	2.0	23.5	13.0	8.5	2.0	8.0	5.0	3.5	0.6	8.0
	3.0	7.0	6.0										
EEB1	17.0	9.0	6.5	0.6	18.0	11.0	6.5	1.3	11.0	6.0	4.5	0.6	5.0
	3.0	8.0	6.0										
EFA1	28.5	17.0	8.5	2.0	22.0	11.0	8.5	2.0	11.5	6.0	4.0	0.6	11.3
	5.3	12.0	6.0										
EFB1	17.5	10.0	8.0	1.3	16.0	10.0	9.0	0.6	9.5	7.0	5.0	0.9	17.0
	4.0	9.0	6.0										
EGA1	31.0	15.0	12.5	4.0	30.0	17.0	12.0	3.3	14.0	9.0	8.0	2.0	13.3
	8.6	8.0	6.0										
EGB1	41.0	20.0	50.0	7.3	40.0	20.0	14.0	4.0	19.5	10.0	7.5	2.9	27.0
	15.0	8.0	8.0										
EGC1	28.5	14.0	8.5	3.3	23.5	12.0	8.5	1.8	14.0	5.0	5.0	2.4	19.0
	9.6	9.0	6.0										
EGD1	33.5	20.0	11.0	4.0	26.5	15.0	10.0	2.6	16.5	15.0	6.0	3.3	21.3
	10.0	11.0	8.0										

B. Floral-achene OTU by character matrix

AAA1	4.0	2.7	2.8	2.0	1.8	0.6	1.3
AAA2	3.6	2.7	2.8	2.0	1.6	0.6	1.3
AAB1	4.0	2.8	2.3	2.0	2.0	0.5	1.3
AAB2	3.5	2.7	2.7	2.1	1.5	0.5	1.3
AAC1	3.6	2.7	2.4	2.0	1.7	0.6	1.3
ABA1	4.0	2.7	2.4	2.0	2.1	0.6	1.3
ABB1	3.4	2.4	2.1	1.6	1.6	0.5	1.1
ACA1	4.5	2.9	2.9	1.9	2.1	1.1	1.9
ACA2	4.5	2.9	3.1	2.3	2.1	0.9	1.6
ACB1	4.1	3.1	3.1	2.3	1.7	0.8	1.3
ACB2	4.1	2.8	2.9	2.1	1.7	0.6	1.6
ACC1	4.1	2.8	2.8	2.0	2.1	0.6	1.3
ACC2	4.4	2.8	2.9	2.0	2.3	0.6	1.3
ADA1	4.4	2.8	2.9	2.1	2.0	0.5	1.7
ADA2	4.0	2.9	2.9	2.3	2.0	0.6	1.6
ADB1	4.0	2.8	2.7	2.0	2.0	0.6	1.3
ADB2	4.4	2.9	2.8	2.1	2.3	0.5	1.3
AEA1	4.5	2.9	3.1	2.4	2.3	0.6	1.6
AEA2	4.8	2.9	3.1	2.3	2.0	0.6	1.7
AEB1	4.0	2.8	2.5	2.1	2.7	0.5	1.6
AEB2	4.1	2.9	2.5	1.9	2.0	0.5	1.6
AEC1	4.1	2.9	2.9	2.1	2.3	0.6	1.6
AEC2	4.8	2.9	3.1	2.1	2.6	0.6	1.5
AFA1	4.4	2.6	2.6	1.8	2.0	0.5	1.3
AFA2	4.2	2.9	2.6	2.0	2.3	0.5	1.6

AFB1	4.4	2.7	2.9	2.1	2.3	0.6	2.1
AFB2	4.6	2.9	3.3	2.3	2.5	0.6	1.9
AFC1	4.7	2.9	3.5	2.0	2.1	0.6	1.9
AFC2	4.1	2.9	3.1	2.3	2.0	0.6	1.6
AFD1	4.2	2.7	2.8	2.0	2.3	0.6	1.6
AFD2	4.1	2.8	3.2	2.0	2.1	0.6	1.6
AGA1	4.0	2.8	2.7	2.0	2.1	0.6	1.3
AGA2	4.3	2.8	2.8	1.9	2.3	0.6	1.3
AGB1	4.0	2.9	2.9	1.9	2.1	0.6	1.1
AGB2	4.0	2.9	2.8	2.1	2.0	0.6	1.3
AGC1	4.6	2.8	3.3	2.1	2.4	0.8	1.6
AGC2	4.2	2.9	3.1	2.3	2.3	1.1	1.6
AGD1	4.6	2.9	2.8	2.3	2.0	0.6	1.3
AGD2	4.1	2.9	2.7	1.7	2.3	0.5	1.1
AGE1	4.2	2.9	2.8	2.1	2.0	0.6	1.3
AGE2	4.0	2.9	2.6	2.0	1.9	0.6	1.3
AHA1	4.8	3.3	2.8	2.0	2.5	0.8	1.9
AHA2	4.8	2.5	3.3	1.7	2.6	0.8	1.7
AHB1	4.8	2.5	3.3	1.7	2.6	0.8	1.7
AIA1	4.1	2.7	2.4	2.0	1.7	0.8	1.3
AIB1	4.0	2.7	3.1	1.9	1.7	0.8	1.6
AJA1	4.4	3.3	2.8	2.3	2.0	0.6	1.6
AJB1	4.4	3.3	2.7	2.1	2.0	0.6	1.3
AJB2	4.6	3.3	2.9	2.1	1.9	0.6	1.6
AJC1	3.7	2.8	2.7	1.8	1.7	0.6	1.3
AJC2	3.8	3.1	2.4	2.0	1.3	0.5	1.3
AKA1	3.7	2.9	2.5	1.9	1.9	0.6	0.8
AKB1	3.6	2.5	2.4	2.0	1.7	0.6	0.8
ALA1	3.6	2.8	2.5	1.9	1.7	0.5	1.3
ALB1	3.2	2.9	2.9	2.1	1.7	0.5	1.1
AMA1	3.7	2.8	2.6	2.1	1.6	0.5	0.9
AMB1	3.6	2.8	2.5	2.0	1.7	0.5	1.3
ANA1	3.9	3.1	2.8	2.1	1.7	0.5	1.1
ANB1	3.5	2.8	2.3	1.9	1.6	0.5	1.1
AOA1	4.1	2.8	3.1	2.1	2.0	0.6	1.1
AOB1	3.9	2.6	2.9	2.0	1.9	0.6	1.1
APA1	3.5	2.7	2.5	1.7	1.7	0.5	0.8
APB1	3.7	2.5	2.7	2.0	1.7	0.5	1.3
AQA1	4.5	2.8	2.8	2.1	2.0	0.8	1.3
AQB1	4.5	2.9	2.9	2.1	2.0	0.8	1.1
ARA1	3.8	2.9	2.5	2.0	1.9	0.6	1.1
ARB1	4.3	2.8	2.7	2.1	2.0	0.5	1.3
ASA1	4.0	2.7	2.9	2.1	1.9	0.6	1.6
ASB1	4.1	2.4	2.6	1.9	1.6	0.5	0.8
ATA1	3.9	2.7	2.8	2.1	1.7	0.6	0.8
ATB1	4.1	2.9	2.7	2.0	2.1	0.6	1.3
AUA1	4.5	2.7	2.8	2.1	2.1	0.8	1.3
AUB1	3.6	2.7	2.4	1.9	2.1	0.4	0.8
AUC1	4.4	3.1	2.8	2.0	2.1	0.6	1.2
AUD1	4.0	2.8	2.7	1.9	1.9	0.5	1.6
AVA1	4.1	2.9	2.8	2.0	2.0	0.8	1.6
AVB1	4.1	2.9	2.8	2.0	2.0	0.8	1.6
AVC1	4.1	2.9	2.5	2.1	1.7	0.7	1.1
BAA1	2.8	2.4	2.5	1.6	1.8	0.9	1.9

BAB1	2.9	2.4	2.5	1.7	2.0	0.9	1.3
BAC1	2.9	2.2	2.5	1.6	1.9	0.9	1.5
BBA1	2.8	2.3	2.5	1.7	1.8	0.8	1.3
BBA2	2.3	2.0	2.3	1.6	1.5	0.7	1.3
BBB1	2.9	2.3	2.4	1.7	1.7	0.7	1.3
BBB2	2.9	2.4	2.4	1.7	2.1	0.9	1.3
BBC1	2.9	2.3	2.4	1.7	1.9	0.8	1.1
BBC2	3.1	2.3	2.6	1.7	2.0	0.8	1.5
BBD1	2.8	2.1	2.3	1.7	1.6	0.9	1.3
BBD2	2.9	2.4	2.4	1.7	1.6	0.9	1.3
BCA1	2.9	2.3	2.7	1.7	1.9	0.9	1.5
BCA2	3.1	2.3	2.5	1.7	2.1	0.9	1.5
BCB1	3.3	2.5	2.4	1.7	2.1	1.1	1.4
BCB2	3.2	2.4	2.7	1.7	2.1	0.9	1.6
BDA1	2.9	2.8	2.4	2.0	1.8	0.9	1.1
BDB1	2.8	2.3	2.4	1.7	1.5	0.9	1.6
BDB2	2.7	2.4	2.5	1.7	1.9	0.8	1.3
BDC1	2.9	2.4	2.5	1.9	2.0	1.1	1.5
BDC2	3.1	2.3	2.4	1.8	1.9	0.9	1.3
BDD1	2.9	2.3	2.4	1.7	1.9	0.9	1.6
BDD2	2.7	2.1	2.3	1.6	1.5	0.9	1.3
BDE1	3.2	1.9	2.1	1.8	2.0	0.9	1.3
BEA1	3.1	2.6	2.5	1.9	1.9	0.9	1.1
BEB1	3.2	2.5	2.4	1.9	2.0	1.1	1.1
BEC1	3.6	2.5	2.5	1.9	2.3	0.9	1.3
BFA1	3.4	2.6	2.5	1.7	2.4	0.9	1.6
BFB1	3.4	2.8	2.5	1.8	2.0	0.8	1.1
BGA1	2.7	2.4	2.4	1.7	2.0	1.1	1.3
BGB1	2.9	2.5	2.3	1.7	1.9	0.9	1.2
BGC1	2.9	2.3	2.5	1.9	1.8	0.9	1.6
BHA1	3.3	2.7	2.7	2.5	2.3	1.1	1.5
BHB1	3.2	2.5	2.4	1.7	1.9	0.9	1.5
BIA1	3.5	2.4	2.9	1.9	1.6	0.9	1.7
BIB1	3.3	2.5	2.7	1.9	2.3	0.9	1.3
BJA1	3.2	2.3	1.8	1.6	1.9	0.8	1.3
BJB1	3.0	2.3	1.8	1.6	1.6	0.8	1.2
BJC1	3.1	2.1	2.1	1.6	2.1	0.7	1.3
EEA1	3.6	2.8	2.4	2.0	2.8	0.8	2.4
EAB1	2.9	2.5	2.5	2.0	1.9	0.8	1.9
EAB2	3.5	3.1	2.8	2.1	2.5	0.9	1.9
EAC1	3.6	2.8	2.4	2.1	2.4	0.9	1.9
EAC2	3.7	2.8	3.2	2.0	2.4	1.2	2.1
EBA1	3.4	2.8	2.3	1.8	2.5	1.5	2.9
EBA2	3.5	2.8	2.3	2.2	2.3	1.3	2.6
EBB1	3.4	2.8	2.3	1.9	2.3	1.3	2.6
EBB2	3.7	2.7	2.7	1.8	2.5	1.4	2.8
EBC1	3.3	2.5	2.0	1.8	2.0	1.4	2.8
EBC2	3.0	2.4	2.0	1.7	2.2	1.2	2.4
EBD1	3.3	2.5	2.4	1.8	2.5	1.3	2.6
EBE1	3.3	2.9	2.2	1.9	2.5	1.3	2.6
EBE2	3.5	2.7	1.9	1.6	2.3	1.2	2.4
EBF1	3.4	2.3	2.5	1.5	2.4	1.4	2.8
EBF2	3.5	2.5	2.5	1.9	2.4	1.4	2.8
ECA1	2.9	2.8	2.7	2.1	2.3	0.9	1.6

ECA2	3.3	2.8	2.9	2.1	2.1	1.1	1.8
ECB1	3.2	2.9	2.5	1.9	2.0	1.0	1.6
ECB2	3.3	3.2	2.1	1.7	2.6	0.9	1.6
ECC1	3.5	2.8	2.4	2.0	2.1	1.2	1.9
ECC2	3.5	2.8	2.6	2.0	2.0	0.9	1.6
ECD1	3.3	3.2	2.1	1.7	2.6	0.9	1.6
ECE2	3.2	2.9	2.4	1.9	2.0	0.8	1.6
ECF1	3.5	2.7	2.2	2.0	2.3	1.2	1.9
EDA1	3.5	2.7	2.2	2.1	2.3	1.2	1.9
EDA2	3.6	2.0	2.6	1.9	2.4	1.3	1.9
EDB1	3.6	3.1	2.1	1.5	2.5	1.2	1.9
EEA1	3.6	2.6	2.5	1.9	2.4	0.9	1.9
EEA2	3.6	3.2	2.5	2.1	2.1	1.1	2.1
EEB1	3.7	2.7	2.7	2.1	2.7	0.9	1.9
EEB2	3.1	2.7	2.7	2.1	2.0	1.2	2.1
EFA1	3.2	2.7	2.4	1.7	2.0	0.9	1.9
EFB1	3.2	2.6	2.4	1.8	1.9	0.8	1.6
EFB2	3.0	2.6	2.3	1.8	1.9	0.8	1.6
EGA1	4.0	3.1	2.5	2.0	2.5	1.7	2.6
EGA2	4.0	3.1	2.5	2.0	2.5	1.7	2.6
EGB1	4.1	3.2	2.8	2.1	2.6	1.6	2.1
EGC1	3.3	2.9	2.8	2.1	2.3	1.1	2.1
EGD1	3.6	2.7	2.8	2.1	2.6	1.6	2.6

Appendix 2. Vegetative, floral and achene OTU by character matrix
including residual values and plant means.

AAA	17.6667	-0.6199	1.8105	-0.0413	0.6922	-0.2275	2.3972	-0.0208
	0.2692	-0.0791	1.2360	-0.1161	8.1000	2.8667	6.6667	4.0000
	3.8000	2.7000	0.2004	0.1156	-0.3640	0.6000	1.3000	
AAB	16.5000	0.4004	1.0588	-0.1978	-0.6925	0.1611	1.9171	-0.1882
	1.0389	0.0458	0.5196	-0.3723	9.3000	5.3000	6.5000	4.0000
	3.7500	2.7500	-0.0748	0.1365	-0.2996	0.5000	1.3000	
AAC	20.0000	-0.6604	0.8138	0.2718	0.9617	-0.5682	2.2400	0.2857
	1.7299	4.7952	1.4713	0.1908	9.0000	5.7000	8.0000	4.0000
	3.6000	2.7000	-0.1004	0.1156	-0.3061	0.6000	1.3000	
ABA	16.0000	-0.3052	2.0223	-0.5649	-1.0002	-0.4079	1.1819	-0.7367
	0.2259	-1.3289	1.1687	-0.4038	9.0000	4.0000	8.0000	4.0000
	4.0000	2.7000	-0.2988	0.1156	-0.0220	0.6000	1.3000	
ABB	12.3000	-0.1267	2.0027	-0.3213	-1.7275	-0.1095	1.0942	-0.5620
	-1.3903	-0.4529	0.8661	-0.2983	5.8000	2.7000	6.0000	3.0000
	3.4000	2.4000	-0.3012	-0.1099	-0.3482	0.5000	1.1000	
ACA	14.7500	0.9308	1.8063	0.2674	1.6054	0.7302	1.9023	0.5103
	2.9434	0.7642	1.5207	0.3921	9.8000	8.5000	7.0000	5.5000
	4.5000	2.9000	0.0532	0.0993	-0.1667	1.0000	1.7500	
ACB	16.0000	0.6948	1.0223	-0.0149	-0.7502	0.4484	1.3436	-0.5038
	0.4759	0.0148	1.0689	0.4791	8.8000	5.3000	7.0000	5.5000
	4.1000	2.9500	0.2516	0.1702	-0.4509	0.7000	1.4500	
ACC	13.2500	0.3140	1.1970	-0.2839	-0.0678	-0.0460	0.4615	-0.1837
	1.2544	0.1711	1.1687	-0.0538	7.6500	3.8000	6.0000	5.5000
	4.2500	2.8000	0.0272	0.0574	0.0057	0.6000	1.3000	
ADA	16.5000	0.4004	1.8088	0.5022	1.0575	1.1556	1.2992	-0.6083
	1.5389	-0.2668	0.5700	-0.4065	9.0000	6.0000	7.0000	4.0000
	4.2000	2.8500	0.1020	0.2284	-0.1799	0.5500	1.6500	
ADB	17.0000	0.1060	1.5952	0.0193	0.1153	-0.0571	0.9758	-0.1740
	1.8519	-0.0795	1.1205	0.1592	10.0500	8.6500	7.0000	4.5000
	4.2000	2.8500	-0.0480	0.0784	-0.0299	0.5500	1.3000	
AEA	20.5000	1.0452	-0.8998	-0.0111	0.2695	-0.9245	-0.9217	-0.0472
	5.2929	-0.0497	-0.7754	-0.0661	9.5000	5.6500	8.5000	4.0000
	4.6500	2.9000	0.0788	0.3493	-0.1602	0.6000	1.6500	
AEB	16.0000	-0.3052	3.0223	-0.6649	0.4998	0.7302	2.1523	-0.1397
	2.7259	0.1078	1.1709	-0.2750	8.0000	8.3000	7.0000	4.0000
	4.0500	2.8500	-0.2236	0.0284	0.2136	0.5000	1.6000	
AEC	18.5000	-0.7772	1.4545	0.7705	-2.2115	1.0175	1.3288	-0.5053
	0.7909	-0.2668	0.5700	-0.4065	10.3000	7.6000	8.0000	6.0000
	4.4500	2.9000	0.0780	0.0993	0.1978	0.6000	1.5500	
AFA	18.5000	-0.7772	2.2045	0.1705	0.2885	-0.4190	2.1962	-0.0770
	3.2909	0.1699	0.5722	0.6223	13.3000	9.9500	7.5000	4.0000
	4.3000	2.7500	-0.2476	-0.0135	-0.0588	0.5000	1.4500	
AFB	17.5000	0.3116	1.1316	0.7364	0.6730	0.3683	0.6227	-0.2427
	3.4149	0.3262	0.9220	-0.0606	14.9500	9.3000	7.0000	4.0000
	4.5000	2.8000	0.1532	0.2574	0.1333	0.6000	2.0000	
AFC	24.7500	-1.9572	2.5349	0.2091	1.0103	-1.0102	2.2394	0.7939
	5.9533	-1.4567	2.0766	0.2798	28.0000	14.0000	8.5000	4.0000
	4.4000	2.9000	0.4028	0.1493	-0.1878	0.6000	1.7500	
AFD	12.2500	-0.0972	1.8741	-0.2681	0.0667	-0.6151	1.2263	-0.2322
	0.6284	-0.2036	0.8178	-0.2353	5.8000	6.1500	6.5000	3.0000

	4.1500	2.7500	0.2268	0.0865	0.0346	0.6000	1.6000	
AGA	21.2500	-0.3964	1.2799	0.6895	-0.3939	0.0755	1.3283	0.2528
	0.5123	-0.2358	1.0207	0.5921	9.3000	6.9500	6.5000	4.0000
	4.1500	2.8000	-0.0232	0.0074	0.0346	0.6000	1.3000	
AGB	16.0000	-1.0552	2.7723	-0.0149	-0.0002	0.0175	2.3288	-0.4553
	1.7259	-0.7668	1.3200	-0.4065	15.8000	14.3000	6.5000	4.0000
	4.0000	2.9000	0.1512	-0.0007	-0.0720	0.6000	1.2000	
AGC	17.5000	-0.1884	2.3816	-0.2636	1.6730	-1.7063	1.7696	0.0887
	1.1649	-1.2668	2.0700	-0.5065	5.3000	6.6000	8.0000	4.0000
	4.4000	2.8500	0.3028	0.2284	0.1122	0.9500	1.6000	
AGD	17.7500	0.1644	2.0249	-0.1801	-0.0481	-0.8444	1.7992	-0.1583
	0.8214	-0.6105	0.6698	-0.0894	10.6500	6.6500	6.5000	4.0000
	4.3500	2.9000	-0.1224	-0.0007	-0.0733	0.5500	1.2000	
AGE	19.0000	-0.5716	2.2409	0.4876	1.0962	0.3628	2.5048	0.6372
	0.8539	0.0768	1.4702	0.6264	11.3000	8.1500	7.5000	4.0000
	4.1000	2.9000	-0.0484	0.0493	-0.2009	0.6000	1.3000	
AHA	16.0000	0.6948	1.5223	-0.1649	1.4998	0.1556	1.7992	-0.6083
	-1.7741	-0.0782	0.9670	-0.1668	9.1000	6.5000	4.0000	4.0000
	4.8000	2.9000	-0.0456	-0.1507	0.1964	0.8000	1.8000	
AHB	13.5000	-0.3332	2.5902	-0.0003	-1.2889	1.0286	1.0646	-0.1650
	4.6609	-0.5175	1.7718	0.0565	7.3000	3.3000	8.0000	4.0000
	4.8000	2.5000	0.2044	-0.0680	0.2464	0.8000	1.7000	
AIA	19.0000	-1.0716	1.7409	-0.0624	-1.1538	1.1556	1.7992	-0.6083
	2.1039	-0.7048	0.9713	0.1908	14.6000	10.3000	8.0000	4.0000
	4.1000	2.7000	-0.3484	0.1156	-0.4509	0.8000	1.3000	
AIB	17.5000	0.8116	1.8816	-0.6636	0.6730	-1.1317	1.6227	-0.7427
	-0.3351	-0.3289	0.6687	-0.3038	5.0000	4.0000	8.0000	4.0000
	4.0000	2.7000	0.4012	0.0156	-0.4220	0.8000	1.6000	
AJA	15.5000	1.4892	1.2359	-0.0320	-0.0580	-0.6952	1.2554	0.0790
	0.6629	-0.4852	1.0689	-0.0209	5.3000	4.5000	7.0000	4.0000
	4.4000	3.3000	-0.0972	0.0666	-0.2378	0.6000	1.6000	
AJB	17.0000	-0.8940	1.0952	-0.2307	0.1153	0.4429	1.4758	-0.1740
	0.8519	-0.9542	0.7696	0.3277	7.8000	7.5000	8.0000	4.0000
	4.5000	3.3000	-0.1468	-0.1334	-0.3167	0.6000	1.4500	
AJC	14.5000	0.0780	2.1630	0.0838	0.3265	0.0921	1.4319	-0.4867
	0.7869	-0.3289	0.9187	-0.1538	8.0500	4.1500	7.5000	4.0000
	3.7500	2.9500	-0.0248	-0.1298	-0.5496	0.5500	1.3000	
AKA	14.0000	-0.1276	2.3766	-0.4332	1.2688	-0.6952	1.5054	-0.1710
	2.9739	0.4205	2.3705	0.0592	11.0000	4.5000	6.0000	4.0000
	3.7000	2.9000	-0.0500	-0.1007	-0.1351	0.6000	0.8000	
AKB	13.0000	0.4612	2.8037	-0.3674	0.1533	0.4540	1.7115	-0.4337
	-0.6521	-0.0782	1.4670	-0.1668	8.0000	2.5000	6.5000	4.0000
	3.6000	2.5000	-0.1004	0.2320	-0.3061	0.6000	0.8000	
ALA	19.0000	-1.0716	1.7409	-0.3624	1.8462	-1.5682	2.2400	0.2857
	1.1039	0.4205	3.3705	0.2592	17.0000	8.0000	9.6000	4.0000
	3.6000	2.8000	-0.0004	-0.0426	-0.3061	0.5000	1.3000	
ALB	23.0000	-1.4268	2.0324	0.0743	1.3082	-0.2920	1.6808	0.0797
	-3.3922	0.2964	1.5678	0.0647	22.0000	4.0000	11.0000	4.0000
	3.2000	2.9000	0.5980	0.0993	-0.1903	0.5000	1.1000	
AMA	13.5000	0.1668	0.0902	0.2997	2.2111	0.0175	2.8288	-0.1053
	2.1609	0.0458	0.2696	-0.1723	10.0000	4.0000	8.5000	4.0000
	3.7000	2.8000	0.0500	0.1574	-0.4351	0.5000	0.9000	
AMB	17.0000	-0.8940	0.5952	-0.6307	-0.3847	0.7302	1.6523	0.1603
	0.3519	-0.1415	0.4691	-0.3380	10.5000	4.5000	6.5000	4.0000

	3.6000	2.8000	-0.0004	0.0574	-0.3061	0.5000	1.3000	
ANA	18.0000	0.5172	0.1681	-0.2965	-0.2693	-0.8444	-0.2008	-0.6083
	0.4779	0.0458	-0.2304	0.1277	14.5000	7.3000	6.5000	4.0000
	3.9000	3.1000	0.1508	-0.0171	-0.3930	0.5000	1.1000	
ANB	21.0000	-0.2492	-0.1133	-0.4940	-1.9228	-2.4190	0.4462	-0.9770
	1.3558	-1.2048	-0.0287	-0.3092	14.0000	8.0000	7.3000	4.0000
	3.5000	2.8000	-0.1508	-0.0426	-0.3772	0.5000	1.1000	
AOA	13.5000	1.1668	1.0902	-0.0003	0.7111	-0.1206	1.3585	-0.1024
	-2.3391	-0.1403	0.5656	0.3359	1.3000	4.5000	5.0000	4.0000
	4.1000	2.8000	0.3516	0.1574	-0.1509	0.6000	1.1000	
AOB	17.0000	-1.8940	1.0952	-0.2307	0.1153	0.4429	0.4758	-0.1740
	1.8519	-0.5795	0.8705	0.0592	6.5000	6.0000	6.5000	4.0000
	3.9000	2.6000	0.2508	0.1738	-0.1930	0.6000	1.1000	
APA	15.0000	1.2836	-0.5505	0.1009	-1.1157	2.1667	1.0350	0.0320
	1.0999	1.3585	-0.0309	0.3620	14.0000	5.3000	6.7000	4.0000
	3.5000	2.7000	0.0492	-0.1844	-0.2772	0.5000	0.8000	
APB	14.0000	0.8724	0.8766	0.2668	1.2688	1.3048	1.0054	-0.0710
	0.9739	0.6711	0.6687	-0.3038	10.6000	4.6000	6.7000	4.0000
	3.7000	2.5000	0.1500	0.2320	-0.3351	0.5000	1.3000	
AQA	33.0000	2.6852	3.7611	1.4161	1.4630	4.5367	-0.9969	0.7618
	3.8677	-0.5820	-0.3225	0.5114	32.6000	15.0000	10.0000	4.0000
	4.5000	2.8000	-0.1468	0.1574	-0.2667	0.8000	1.3000	
AQB	26.0000	-0.1932	-2.2490	-0.0231	0.6546	0.5588	-1.5254	-0.0576
	6.4858	2.4180	-2.3225	0.4114	12.0000	8.3000	10.0000	4.0000
	4.5000	2.9000	-0.0468	0.0993	-0.2667	0.8000	1.1000	
ARA	19.0000	2.9284	1.2409	0.3376	1.8462	2.4318	1.2400	-0.0143
	5.6039	-0.3934	0.5744	-0.2489	10.0000	10.6000	8.0000	4.0000
	3.8000	2.9000	-0.0996	-0.0007	-0.1640	0.6000	1.1000	
ARB	16.5000	0.4004	0.8088	-0.3978	-0.9425	1.3048	1.5054	-0.7710
	1.0389	1.0458	1.2696	-0.3723	12.6000	8.0000	6.6000	4.0000
	4.3000	2.8000	-0.1476	0.1574	-0.2088	0.5000	1.3000	
ASA	19.5000	-0.3660	2.0274	-0.3953	-2.5960	-0.2698	2.1523	-0.8397
	-0.0831	0.0458	1.2696	-0.3723	8.6000	6.6000	10.0000	6.0000
	4.0000	2.7000	0.2012	0.2156	-0.2220	0.6000	1.6000	
ASB	18.0000	1.5172	0.1681	0.4035	-0.2693	1.1556	0.2992	0.0917
	0.9779	-0.2668	1.5700	-0.4065	8.6000	5.6000	6.0000	4.0000
	4.1000	2.4000	-0.1484	0.1901	-0.5509	0.5000	0.8000	
ATA	12.0000	1.0500	2.2309	-0.3016	-0.4622	1.3159	1.7411	-0.0307
	0.2219	-0.3909	0.7674	0.0989	8.0000	4.6000	4.7000	4.0000
	3.9000	2.7000	0.1508	0.2156	-0.3930	0.6000	0.8000	
ATB	17.5000	-0.1884	2.8816	-0.2636	0.1730	1.1556	1.7992	0.0917
	1.6649	0.4205	1.3705	-0.1408	13.3000	10.3000	6.6000	4.0000
	4.1000	2.9000	-0.0484	-0.0007	-0.0509	0.6000	1.3000	
AUA	26.5000	4.5124	2.0375	-0.1560	2.7124	4.1224	0.0919	0.3707
	0.2988	-0.8301	0.0722	0.1223	20.6000	16.3000	8.0000	4.0000
	4.5000	2.7000	-0.1468	0.2156	-0.1667	0.8000	1.3000	
AUB	20.0000	0.3396	0.3138	-0.8282	0.9617	0.4318	-0.2600	-0.4143
	1.2299	1.1078	-0.3291	0.4250	15.3000	6.7000	6.7000	4.0000
	3.6000	2.7000	-0.1004	0.0156	0.0939	0.4000	0.8000	
AUC	25.0000	0.3956	2.1782	-0.0573	1.0391	0.8461	0.6512	-0.7233
	1.3598	0.8572	-0.1273	0.7880	20.6000	14.6000	8.0000	6.0000
	4.4000	3.1000	-0.0972	-0.1171	-0.1378	0.6000	1.2000	
AUD	23.0000	3.5732	-0.4676	0.4743	1.3082	3.7080	-0.3192	0.0797
	1.6078	1.1699	0.0722	0.4223	19.3000	11.0000	8.0000	6.0000

	4.0000	2.8000	0.0012	-0.0426	-0.2220	0.5000	1.6000	
AVA	20.0000	2.3396	-0.1862	0.2718	-0.5383	2.2937	0.7696	-0.3113
	-2.2701	1.2964	0.0678	-0.3353	11.6000	3.0000	8.0000	4.0000
	4.1000	2.9000	0.0516	-0.0007	-0.1509	0.8000	1.6000	
AVB	20.0000	2.3396	-0.1862	0.2718	-0.5383	2.2937	0.7696	-0.3113
	-2.2701	1.2964	0.0678	-0.3353	11.6000	3.0000	8.0000	4.0000
	4.1000	2.9000	0.0516	-0.0007	-0.1509	0.8000	1.6000	
AVC	20.0000	1.3396	0.3138	0.2718	0.9617	2.4318	0.2400	0.2857
	0.2299	1.2332	0.0700	0.0935	10.3000	4.3000	8.0000	6.0000
	4.1000	2.9000	-0.2484	0.0993	-0.4509	0.7000	1.1000	
BAA	18.0000	0.5172	-1.8319	0.4035	0.7307	-0.4190	-1.5538	0.4230
	0.9779	-0.7668	-1.4300	-0.4065	14.0000	6.4000	6.0000	4.0000
	2.8000	2.4000	0.3964	-0.1099	0.0255	0.9000	1.9000	
BAB	18.0000	0.5172	-1.8319	0.4035	-0.2693	0.1556	-0.7008	0.0917
	-0.5221	0.6711	-0.8313	-0.0038	11.5000	5.5000	6.5000	4.0000
	2.9000	2.4000	0.3468	-0.0099	0.1965	0.9000	1.3000	
BAC	16.0000	-0.3052	-0.9777	-0.1649	1.4998	0.1556	-2.2008	0.3917
	1.2259	-1.9542	-1.7304	-0.3723	12.6000	4.4000	6.0000	4.0000
	2.9000	2.2000	0.3468	0.0065	0.0965	0.9000	1.5000	
BBA	17.5000	0.8116	-0.1184	-0.3636	0.1730	1.1556	0.7992	1.0917
	-1.3351	0.2964	-0.9322	0.0647	9.5000	3.3000	7.0000	4.0000
	2.5500	2.1500	0.4204	0.0856	-0.0521	0.7500	1.3000	
BBB	16.5000	0.4004	-0.6912	0.5022	0.5575	0.4429	-1.5242	0.2260
	-0.4611	-0.0162	0.3683	0.0305	8.6000	5.0000	6.0000	4.0000
	2.9000	2.3500	0.2468	0.0192	0.0965	0.8000	1.3000	
BBC	13.5000	0.1668	-0.4098	-0.0003	0.7111	0.8794	-0.6415	0.1976
	3.6609	0.1078	-1.3291	0.0250	9.3000	3.0000	6.0000	4.0000
	3.0000	2.3000	0.2972	0.0483	0.1176	0.8000	1.3000	
BBD	12.0000	1.0500	0.2309	0.2984	-0.9622	-1.3968	-0.5823	0.1036
	1.2219	0.9838	-0.6317	-0.0695	6.3000	3.0000	7.0000	6.0000
	2.8500	2.2500	0.2216	0.0774	-0.1890	0.9000	1.3000	
BCA	17.0000	-1.8940	-1.4048	-0.7307	0.6153	0.1556	-2.2008	-0.2083
	-1.6481	-0.3909	-0.7326	-0.3011	16.0000	7.0000	6.0000	4.0000
	3.0000	2.3000	0.3972	0.0483	0.1676	0.9000	1.5000	
BCB	21.0000	-2.2492	-1.1133	-0.4940	1.5772	0.5699	-1.7896	-0.1173
	0.8558	-0.8922	-1.8291	-0.1750	15.3000	5.7000	7.0000	6.0000
	3.2500	2.4500	0.2232	-0.0390	0.1952	1.0000	1.5000	
BDA	17.0000	-0.8940	-0.4048	-0.2307	-1.3847	0.3048	-0.4946	-0.1710
	2.8519	-0.2048	-0.5287	-0.0092	13.0000	5.7000	6.0000	6.0000
	2.9000	2.8000	0.2468	0.0574	-0.0035	0.9000	1.1000	
BDB	15.0000	0.2836	-0.0505	-0.2991	0.3843	0.3048	-0.9946	-0.1710
	1.0999	0.3585	-0.5309	-0.1380	9.5000	3.5000	5.0000	4.0000
	2.7500	2.3500	0.3712	0.0192	-0.0600	0.8500	1.4500	
BDC	15.0000	-1.7164	0.9495	-0.5991	-0.1157	-0.4079	-0.3181	-0.2367
	-1.4001	-0.0782	-0.5330	0.1332	7.0000	2.0000	5.0000	4.0000
	3.0000	2.3500	0.2472	0.1692	0.1176	1.0000	1.4000	
BDD	17.0000	0.1060	-1.4048	-0.2307	-1.8847	-0.4079	-1.8181	-0.0367
	-2.1481	-0.0782	-1.5330	-0.1668	14.0000	5.3000	6.0000	6.0000
	2.8000	2.2000	0.2464	0.0565	-0.0745	0.9000	1.4500	
BDE	18.5000	-0.7772	-0.5455	-0.3295	-0.2115	-0.1317	-0.8773	-0.4427
	2.7909	-1.5175	-1.2282	-0.3435	12.0000	4.6000	7.0000	6.0000
	3.2000	1.9000	-0.2020	0.3810	0.1097	0.9000	1.3000	
BEA	21.0000	0.7508	-4.1133	-0.1940	-2.4228	-0.1317	-3.3773	-0.4427
	-3.6442	-0.0782	-1.0330	-0.1668	17.3000	3.0000	7.3000	4.0000

	3.1000	2.6000	0.2476	0.0738	0.0386	0.9000	1.1000	
BEB	23.5000	1.2788	-3.6811	1.3414	0.8659	1.7080	-3.8192	0.3797
	-0.5792	0.4205	-2.6295	0.2592	15.0000	6.3000	6.7000	4.0000
	3.2000	2.5000	0.0980	0.1320	0.1097	1.1000	1.1000	
BEC	22.5000	2.8676	-2.7540	-0.1927	1.7504	1.7080	-2.8192	0.0797
	-0.2052	-0.5795	-1.6295	-0.1408	19.3000	3.3000	7.3000	4.0000
	3.6000	2.5000	-0.0004	0.1320	0.2939	0.9000	1.3000	
BFA	25.5000	-3.8988	-3.5354	0.6098	1.0969	-0.4412	-2.5254	-0.0576
	0.6728	-1.8301	-0.9278	-0.2777	21.3000	6.0000	7.3000	4.0000
	3.4000	2.6000	0.0988	-0.1262	0.4518	0.9000	1.6000	
BFB	23.0000	0.5732	-3.9676	0.0743	1.8082	3.4207	-3.4958	0.0454
	-0.3922	-0.5795	-0.6295	0.2592	17.0000	5.0000	6.6000	4.0000
	3.4000	2.8000	0.0988	-0.1426	0.0518	0.8000	1.1000	
BGA	17.0000	-1.8940	-0.9048	0.1693	-1.3847	1.3048	-0.9946	0.4290
	0.3519	-1.6415	-1.5309	-0.0380	12.6000	3.5000	6.7000	6.0000
	2.7000	2.4000	0.3460	-0.0099	0.2545	1.1000	1.3000	
BGB	15.5000	0.9892	-1.2641	-0.1320	-0.0580	-1.6952	-0.9946	-0.4710
	-0.5871	-0.7036	-0.4322	-0.0353	2.5000	3.0000	5.5000	4.0000
	2.9000	2.5000	0.1468	-0.0680	0.0965	0.9000	1.2000	
BGC	13.0000	-0.5388	-1.1963	-0.3674	0.1533	-0.5460	-1.7885	-0.3337
	-0.6521	-0.0782	-1.0330	-0.1668	9.3000	3.0000	5.5000	4.0000
	2.9000	2.3000	0.3468	0.2483	-0.0035	0.9000	1.6000	
BHA	21.0000	-2.2492	-3.6133	0.2060	-3.9228	-2.2698	-2.8477	-0.1397
	-4.6442	-0.4529	-0.6339	-0.0983	12.5000	3.0000	7.0000	4.0000
	3.3000	2.7000	0.3484	0.6156	0.3807	1.1000	1.5000	
BHB	17.0000	0.1060	-3.4048	-0.2307	-2.3847	-1.1206	-2.6415	-0.0024
	-5.1481	-0.2023	-0.3357	-0.0614	9.0000	2.5000	5.5000	4.0000
	3.2000	2.5000	0.0980	-0.0680	0.0097	0.9000	1.5000	
BIA	20.0000	0.3396	-3.1862	-0.0282	2.9617	-0.7174	-3.9661	-0.1516
	-1.2701	0.1711	-1.3313	-0.3038	14.0000	2.5000	8.0000	4.0000
	3.5000	2.4000	0.4492	0.1901	-0.3772	0.9000	1.7000	
BIB	18.0000	-1.4828	-2.3319	-0.2965	-0.2693	-0.8444	-2.2008	-0.2083
	-3.0221	-0.7656	-1.3335	-0.1326	11.6000	2.6000	6.0000	6.0000
	3.3000	2.5000	0.3484	0.1320	0.3807	0.9000	1.3000	
BJA	17.5000	-2.1884	-3.6184	0.4364	-6.8270	0.1778	-1.7293	0.2723
	-3.3351	0.5471	-0.1339	0.6017	9.6000	7.0000	9.4000	6.0000
	3.2000	2.3000	-0.5020	-0.0517	0.0097	0.8000	1.3000	
BJB	16.0000	0.6948	-1.4777	0.5351	4.9998	-2.8555	-3.4365	-0.4486
	-0.7741	-0.7036	-0.9322	-0.2353	12.6000	6.0000	7.3000	4.0000
	3.0000	2.3000	-0.4028	-0.0517	-0.2324	0.8000	1.2000	
BJC	14.0000	-0.1276	-1.6234	0.6668	-0.7312	0.4540	-2.2885	-0.3337
	-3.0261	0.1724	-0.7348	0.5702	9.3000	4.6000	6.6000	4.0000
	3.1000	2.1000	-0.1524	0.0646	0.2386	0.7000	1.3000	
EAA	26.7500	-1.1348	-1.3193	-0.2225	3.9912	-0.7395	-0.6877	-0.1823
	-5.2947	0.6091	0.0174	-0.2011	9.0000	4.0000	7.5000	7.0000
	3.6000	2.8000	-0.1004	0.0574	0.7939	0.8000	2.4000	
EAB	31.5000	-0.4316	-1.5982	-0.6852	2.5398	-1.3197	0.0914	-0.5211
	-6.0712	0.4838	0.3683	-0.2695	11.0000	3.5000	7.5000	8.5000
	3.2000	2.8000	0.3480	0.1074	0.3097	0.8500	1.9000	
EAC	38.2500	0.0940	-1.7314	-1.0795	2.8193	-1.9109	0.3847	-0.9502
	1.9042	2.4180	-0.3225	-0.8886	12.2500	5.7500	12.5000	8.5000
	3.6500	2.8000	0.2748	0.1074	0.3794	1.0500	2.0000	
EBA	34.5000	4.8020	-0.8796	0.6174	3.1362	3.3129	0.4439	0.1558
	7.8067	-0.3959	-1.6186	0.1032	15.6000	11.6500	17.0000	9.0000

	3.4500	2.8000	-0.1260	0.0574	0.4373	1.4000	2.7500	
EBB	37.0000	-4.1700	-0.4474	-0.1972	0.9250	-2.6871	-1.5561	-0.0942
	1.1217	-0.8004	-0.3236	-0.2530	10.1000	6.0000	9.0000	7.0000
	3.5500	2.7500	0.0244	-0.0635	0.4083	1.3500	2.7000	
EBC	38.5000	1.4468	0.9119	-0.6959	-1.1518	-0.2562	3.9587	-0.6927
	2.5607	1.4490	0.3781	0.1100	13.0000	5.9000	12.5000	9.5000
	3.1500	2.4500	-0.2772	0.0110	0.2242	1.3000	2.6000	
EBD	38.2500	2.5940	1.0186	-1.1795	0.5693	1.3819	0.9291	-1.0457
	-2.8458	2.3882	0.0733	0.2367	8.9000	4.5000	11.0000	9.0000
	3.3000	2.5000	0.0484	0.0320	0.5807	1.3000	2.6000	
EBE	25.2500	0.7484	0.5714	-0.5738	0.3180	-1.3666	1.5777	-0.7390
	-0.2337	-0.2048	0.2213	0.1408	8.5000	5.0000	10.5000	8.5000
	3.4000	2.8000	-0.3512	-0.1926	0.4518	1.2500	2.5000	
EBF	34.0000	-1.4036	1.8340	-0.6497	2.5785	0.3875	2.5470	-1.1756
	6.4937	-1.4580	0.9801	-0.2941	19.7500	11.4000	11.0000	9.0000
	3.4500	2.4000	0.0740	-0.0099	0.4373	1.4000	2.8000	
ECA	34.5000	-0.1980	-1.8796	-0.6826	-3.6138	0.6914	-0.4229	-0.8808
	-1.9433	0.2009	0.2729	-0.2291	13.1500	8.5000	9.5000	9.0000
	3.1000	2.8000	0.5476	0.1574	0.3386	1.0000	1.7000	
ECB	21.7500	-2.6908	1.5663	-0.5434	0.9138	-2.9301	2.2104	-0.5673
	2.0753	1.1699	0.0722	-0.4277	16.1000	10.0000	9.5000	9.5000
	3.2500	3.0500	-0.0268	-0.2880	0.3952	0.9500	1.6000	
ECC	24.5000	0.6900	-1.1083	-0.4244	1.9814	0.5588	-1.0254	-0.9576
	-1.4532	0.7332	0.5700	-0.2065	15.0000	3.5000	8.0000	9.0000
	3.5000	2.8000	0.0492	0.0574	0.0728	1.0500	1.7500	
ECD	22.5000	-0.1324	-0.2540	-0.5927	6.7504	-0.1649	0.4154	-0.9636
	6.7948	-1.9567	-0.9234	-0.6202	13.5000	8.0000	9.0000	8.0000
	3.3000	3.2000	-0.2516	-0.4752	0.6807	0.9000	1.6000	
ECE	30.0000	-0.0484	-1.4575	-0.7864	-5.6334	0.1390	-0.0544	-0.7188
	6.9898	-0.8326	-1.1208	-0.7756	18.1500	7.1000	8.0000	9.0000
	3.2000	2.9000	0.0980	-0.1007	0.1097	0.8000	1.6000	
ECF	28.0000	3.6292	0.8968	-0.9548	-1.1144	-0.4412	2.9746	-0.7576
	3.7378	-1.3314	0.9757	-0.2517	16.0000	13.0000	7.0000	9.0000
	3.5000	2.7000	-0.2508	0.1156	0.3228	1.2000	1.9000	
EDA	24.0000	0.4844	-1.1447	0.3085	2.6737	1.9152	-0.3636	0.2252
	-2.7662	0.6711	-0.3313	-0.2038	15.5000	2.0000	8.0000	7.5000
	3.5500	2.3500	-0.0756	0.3192	0.3583	1.2500	1.9000	
EDB	31.5000	1.0684	-4.0982	0.4648	-0.7102	0.5478	-3.0111	0.6521
	-8.5712	0.5471	-0.8839	0.0517	9.3000	2.5000	7.5000	6.0000
	3.6000	3.1000	-0.4004	-0.6171	0.4939	1.2000	1.9000	
EEA	27.5000	-1.0764	-2.3897	-0.2219	-2.1722	-0.5793	-0.4958	0.0454
	-7.0752	0.5471	0.3661	-0.0983	8.0000	3.0000	7.0000	6.0000
	3.6000	2.9000	-0.0004	-0.0007	0.2439	1.0000	2.0000	
EEB	17.0000	-0.8940	0.0952	-0.9307	1.6153	0.5810	-0.5538	-0.2770
	-0.1481	-0.3289	0.1687	-0.3038	5.0000	3.0000	8.0000	6.0000
	3.4000	2.7000	0.2988	0.2156	0.4018	1.0500	2.0000	
EGA	31.0000	-3.1372	0.1154	1.5477	1.2320	-0.3141	0.7093	0.8991
	-2.3842	0.7952	2.4713	0.8908	13.3000	8.6000	8.0000	6.0000
	4.0000	3.1000	-0.1988	-0.1171	0.3780	1.7000	2.6000	
EGB	41.0000	-4.0252	33.3440	4.1895	2.3869	-3.0601	-0.8215	0.9125
	-0.6243	-1.6440	-0.2238	1.4141	27.0000	15.0000	8.0000	8.0000
	4.1000	3.2000	0.0516	-0.0752	0.4491	1.6000	2.1000	
EGC	28.5000	-2.6652	-2.8168	1.0123	-3.0567	-1.5793	-0.4958	-0.1546
	-1.4492	-3.2048	-0.5287	1.2908	19.0000	9.6000	9.0000	6.0000

	3.3000	2.9000	0.4484	0.0993	0.3807	1.1000	2.1000	
EGD	33.5000	0.3908	-2.4525	1.3832	-4.4792	-0.3031	-0.0550	0.4394
	-0.8193	5.2319	-0.5265	2.0195	21.3000	10.0000	11.0000	8.0000
	3.6000	2.7000	0.2996	0.2156	0.5939	1.6000	2.6000	

Appendix 3. Phenological data.

A. Collections used in phenology experiment.

D.S. Katz 324, 325, 326, 327, 329, 330, 331, 332, 333, 335, 367, 368, 429, 444, 446, 447; *L.L. Consaul & L. Goodfellow* 718, 721, 725, 726; *De Stephano* 285 (WIS); *D.F. Brunton* 6118 (DAO); *S.R. Downie & D.S. Katz* 750 (DAO); *M.J. Oldham & G.M. Allen* 6800 (UTM 764209); *S.R. Hill* 10787 (MICH); *M.J. Oldham & J.P. Prevett* 4118 (UTM 650233);

B. OTU by character matrix for height at flowering and time to flower initiation in weeks following germination. (First letter in OTU code represents the taxon: A = *P. achoreum*, B = *P. buxiforme*, and E = *P. erectum*.)

A324	5.77	6.0	ETH2	22.50	9.0
A325	5.49	6.0	EWI2	21.00	9.0
A326	4.57	6.0	EHOW	12.20	5.0
A327	5.45	6.0	EDAL	22.00	7.0
A329	5.10	6.0			
A330	4.42	6.0			
A331	4.12	6.0			
A332	7.67	6.0			
A333	3.88	6.0			
A335	5.78	6.0			
A367	5.21	6.0			
A368	5.03	6.0			
A718	5.50	6.0			
A721	5.50	6.0			
A725	4.57	6.0			
A726	4.21	6.0			
A285	4.88	6.0			
A429	7.31	6.0			
A444	5.60	6.0			
A446	5.50	6.0			
A447	8.44	6.0			
A481	7.42	6.0			
A718	4.10	6.0			
A721	5.35	6.0			
A726	4.93	6.0			
A750	5.13	6.0			
A680	5.68	6.0			
E331	18.17	7.0			
E363	39.00	9.0			
E300	21.86	9.0			
E360	16.75	7.0			
EHLL	17.00	6.0			
E937	9.75	9.0			
EWI1	25.00	9.0			
ETH1	22.00	9.0			