AN ABSTRACT OF THE THESIS OF

J. Stephen Shelly for the degree of Master of Science in Botany and Plant Pathology presented on April 11, 1985.

Title: Biosystematic Studies of *Phacelia capitata* (Hydrophyllaceae), a Species Endemic to Serpentine Soils in Southwestern Oregon

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Abstract approved: ________________________________
Kenton L. Chambers

Phacelia capitata Kruckeberg is a member of the *Phacelia magellanica* polyploid complex (species group *Magellanicae*), a group of wide-ranging, polymorphic perennials in western North America related to the South American *P. secunda* (= *P. magellanica*). The purpose of this project was to determine, to the extent possible, the interrelationships of *P. capitata* within the *Magellanicae*, using studies of its distribution, cytology, morphology, reproductive biology, and population ecology.

Phacelia capitata is endemic to ultramafic (serpentine and peridotite) outcrops, or similar metamorphic substrates, in Coos, Douglas, and Jackson Counties, southwestern Oregon. Field surveys revealed 22 extant populations. The species occurs on open serpentine slopes, outcrops, and roadbanks or similarly disturbed sites, generally in areas with a south to southeast exposure. The native plant community with which *P. capitata* is frequently

associated is a Pinus jeffreyi/grass savanna.

Soils from five P. capitata sites and two P. corymbosa sites were chemically analyzed. At six of these locations the soils were derived from fully serpentinized parent materials, and were found to possess low levels of phosphorus and very low calcium/magnesium ratios when compared to an eighth sample from a non-serpentine soil. A soil sample from one P. capitata site, derived from a metamorphic rock similar in appearance to serpentine, had chemical characteristics intermediate between those of serpentine and non-serpentine soils.

Chromosome counts from 20 P. capitata populations revealed the existence of diploids (n=11) at 19 of them; tetraploid (n=22) counts were obtained from two populations, one of these populations also containing diploids.

Taximetric studies of living plants from 26 Phacelia populations verify the morphological distinctiveness of P. capitata when compared to P. corymbosa, P. hastata, and P. heterophylla ssp. virgata. Phacelia capitata is most readily distinguished from the other species by its narrow, mostly entire, silvery-pubescent rosette leaves, its often capitate or sub-capitate cyme branches, and its sparse, obscure glandulosity.

Significant seed set in P. capitata does not occur in the absence of insect visitors. When natural pollinators collect nectar from the congested flowers, it is likely that self-pollination between adjacent flowers of an inflorescence is predominant (geitonogamy). However, cross-pollination occurs to some extent in members of the *Magellanicae*, as evidenced by hybridization and introgression at the tetraploid level.

The origin of the polyploids of *P*. *capitata* is problematic. It is possible that *P*. *capitata* may have interbred in the past with *P*. *heterophylla* ssp. *virgata*, or with a more southerly member of the complex, *P*. *egena*. There is also some morphological evidence that *P*. *capitata* may have occasionally hybridized with *P*. *hastata*. However, no plants have been found that suggest any hybrid contact between *P*. *capitata* and *P*. *corymbosa*.

At many locations there has been an increase in numbers of *P*. *capitata* following habitat disturbance, and this appears to have "released" the species from any paucity that formerly characterized its populations. The species evidently possesses poor competitive ability in the more closed vegetation which exists on non-serpentine soils, and also appears to be a poor competitor even in some undisturbed serpentine communities.

Owing to its favorable response to disturbance, *P*. *capitata* is not endangered with extinction. However, it should be maintained on a monitoring list, because of its very narrow geographic distribution and restriction to serpentine or sub-serpentine soils.

Biosystematic Studies of *Phacelia capitata* (Hydrophyllaceae), a Species Endemic to Serpentine Soils in Southwestern Oregon

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed April 11, 1985

Commencement June 1985

APPROVED:

Redacted for privacy

Professor of Botany and Plant Pathology in charge of major

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Dean of Graduate School

Date thesis is presented April 11, 1985

Typed by J. Stephen Shelly

ACKNOWLEDGEMENTS

I wish to thank my major professor, Dr. Kenton L. Chambers, for his help and guidance during all phases of this project. His encouragement, and his frequent sharing of knowledge, are greatly appreciated.

I also wish to thank the other members of my committee, Drs. Robert Frenkel, Mark Wilson, and Roger Petersen, for the careful reading of the thesis which they did on fairly short notice.

Loan specimens were kindly provided by curators of the following herbaria: Museum of Natural History, University of Oregon (ORE); California Academy of Sciences/Dudley Herbarium (CAS/DS); University of Washington (WTU); Humboldt State University (HSC); University of California, Berkeley (UC); and the Jepson Herbarium of the University of California (JEPS).

Support, research, and travel funds, provided by Dr. Thomas C. Moore of the Department of Botany and Plant Pathology and the Oregon State University Herbarium, are gratefully acknowledged. Funds for computer analysis were provided by the Committee for Unsponsored Research, Milne Computer Center, Oregon State University.

Insect taxa were identified by Drs. John D. Lattin, Andrew R. Moldenke, and William P. Stephen, Department of Entomology, Oregon State University.

Assistance with the computer analysis was provided by Drs. C. David McIntire, Robert Frenkel, and Steve Broich.

An enjoyable day of field work was spent with Mr. Russ Holmes, Bureau of Land Management (Roseburg), who provided information on locations of Phacelia capitata sites.

I owe special thanks to LaRea Johnston, for her advice and expertise in many respects. These have especially included completion of the photographic work, and assistance in purchasing my pick-up truck! Special thanks also go to Bob Meinke, who befriended me soon after my arrival in Oregon, and who has taught me much about the flora of the state; and Mark Nelson, who provided valuable field assistance, and made many interesting Phacelia collections in southwestern Oregon.

Without the encouragement, advice, and companionship of many fellow graduate students, past and present, this thesis could never have been completed. These very special friends, among many I am sure, include: Joe Antos, Nancy Fredricks, Dan Luoma, Teresa Magee, Bill Ripple, Glenn Stewart, and Carolyn Wright.

My sincere thanks are especially for Ginger King, who unselfishly provided encouragement, and listened with wonderful patience (which I fear I may have tried on occasion!) to all my concerns over the last six months.

This thesis is dedicated to my parents, John and Lois Shelly, for all their love, support, and understanding, and for fostering my interest in the natural world. To them I am grateful for the gifts of all I have seen and experienced.

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INTRODUCTION

Phacelia capitata Kruckeberg is a perennial species belonging to the *P. magellanica* polyploid complex (species group *Magellanicae*), a wide-ranging group of species in western North America having affinities with the South American species *P. secunda* (=*P. magellanica*). The members of the group are morphologically defined as being those plants of subgenus *Phacelia* which are biennials or perennials, and which possess entire leaves, or pinnately divided leaves with entire divisions or leaflets, and an ovary with four ovules, two to each placenta (Heckard, 1960).

The members of the species group *Magellanicae* form a polyploid pillar complex which has, as its foundation, six species occurring at the base chromosome number of x=11, including *P. capitata*. In his detailed study of the group, however, Heckard (1960) made no attempt to determine the interrelationships of *P. capitata* within the complex.

Phacelia capitata is restricted to serpentine soils over a small geographic area in southwestern Oregon. Due to its rarity, it has received attention as a potentially endangered species and has been placed on various state and federal lists of such species.

This study was undertaken to assess various aspects of the distribution, cytology, ecology, reproductive biology, and morphological characteristics of *P. capitata*. To the extent possible, natural populations of other species in the complex (*P. corymbosa*, *P. hastata*, and *P. heterophylla*) were considered in an attempt to determine the interrelationships of *P. capitata* within the *Magellanicae*. In addition, it is hoped that the information obtained can be used to evaluate the endangerment status of *P. capitata* and to make recommendations for managing the species.

TAXONOMIC RELATIONSHIPS

The Hydrophyllaceae forms a relatively small but widespread family. Taxonomists differ in their opinions regarding the number of genera and species it contains. Munz (1959) suggested that the family contains about 25 genera and 300 species. More recently, Cronquist (1981) stated that the Hydrophyllaceae comprises about 20 genera and 250 species. Constance and Chuang (1982) refer to 18 genera and approximately 326 species.

The family is most common in dry habitats of the western United States (Cronquist, 1981). Of the 18 genera recognized by Constance (1963), 16 are primarily confined to North America, (exceptions are Nama, Phacelia, and Wigandia, which have outlying species in South America, with Nama represented as well from the Hawaiian Islands). Hydrolea is pantropical, and Codon is restricted to South Africa.

The Hydrophyllaceae has had a varied taxonomic history, which was reviewed by Constance (1963) and is summarized as follows.

Jussieu (1789) accounted for five of the genera that are now assigned to the family. Of these, he placed three (Hydrophyllum, Phacelia, and Ellisia) in the family Boraginaceae, and two (Hydrolea and Nama) in the family Convolvulaceae. Brown (1818) separated the former three genera as the order Hydrophylleae and the latter two as the family Hydroleae. The Hydroleae, as monographed by

Choisy (1833), contained Hydrolea, Nama, Romanzoffia, and Wigandia; Eriodictyon was added later (1846). De Candolle (1845) described the genus Codon.

Finally, all the above genera were united into the family Hydrophyllaceae by Gray (1875). He added the genus Tricardia, and later Lemmonia, and divided the family into four tribes. Since that time, the familial relationships of the Hydrophyllaceae have been debated, surely due to the fact that, as Constance (1963) stated, "(t)o some extent the family appears to be a collection of morphological and geographical odds-and-ends." Baillon (1890) submerged the Hydrophyllaceae under the Boraginaceae, but this classification was not accepted. Brand (1913) restored the Hydrophyllaceae to family status.

More recently, contrasting classifications by Thorne (1976) and Cronquist (1981) illustrate the continuing difficulties in interpreting the closest familial relationships of the Hydrophyllaceae. The former aligns the family with the Boraginaceae, while the latter places it closest to the Polemoniaceae. Cronquist (1981) summarizes his interpretation of the problem:

> The Hydrophyllaceae have usually been considered to be allied to the Polemoniaceae on the one hand, and to the Boraginaceae, on the other. I agree. For purposes of formal classification, I find it useful to associate the Hydrophyllaceae with the Polemoniaceae, and to put the Boraginaceae in an allied order. This arrangement helps in the construction of orders that have a reasonable degree of morphological coherence.

Despite its problematic relationships, the

Hydrophyllaceae is characterized by the following traits. The members are herbs or seldom (Eriodictyon, Wigandia) shrubs, often rough-hairy in vestiture; the leaves are alternate or sometimes partly or wholly opposite, simple and entire to pinnately cleft, compound, or dissected, rarely palmately compound; the flowers are solitary, or more often in variously modified, often helicoid cymes, perfect, sympetalous, and generally pentamerous; the calyx is cleft to the middle, or more commonly to the base or nearly so; the corolla is regular or nearly so; the stamens are as many as and alternate with the corolla lobes, attached toward the base or well up in the tube, very often flanked by a pair of small scales; the gynoecium is of two carpels united to form a compound, superior or rarely half-inferior, mostly unilocular ovary; the style is terminal, usually deeply bifid, sometimes cleft essentially to the base, or undivided; the stigmas are mostly capitate; placentae are two, parietal or sometimes axile; the fruit is generally a capsule, or sometimes irregularly dehiscent or indehiscent (Cronquist, 1981).

Constance (1963) summarized the taxonomic history of the genus Phacelia. Bentham (1837) recognized two genera, Phacelia and Eutoca. De Candolle (1845) was responsible for the genera Microgenetes (=Euglypta), Cosmanthus, and Miltitzia. Gray (1875) combined all of these but Miltitzia into Phacelia. Further classifications, based on cytological and other evidence, were subsequently produced by various students of the genus. Finally, Constance (1963) suggested, on the basis of extensive cytological surveys, that a "...natural arrangement can be achieved with the recognition of the three subgenera *Cosmanthus* (x=9), *Howellanthus* (x=8), and *Phacelia* (x=11)." Most recently, Cronquist *et al*. (1984) recognize four sections in their treatment of the genus: *Eutoca*, *Euglypta* (=*Microgenetes*), *Miltitzia*, and *Phacelia*. However, the classification put forth by Constance will be followed here.

Phacelia is by far the largest genus in the family, with approximately 200 species (Constance and Chuang, 1982). It consists of a diverse array of annual and perennial, taprooted herbaceous species; the flowers are borne in helicoid cymes, these often aggregated into a compound inflorescence; the calyx is divided nearly to the base; the corollas are variously blue or purple to pink, white, or yellow, and tubular or rotate; the filaments are attached to the corolla tube near its base; the styles are shortly to very deeply cleft; the capsules are loculicidal; the leaves are entire to pinnately dissected, and chiefly or wholly alternate. The genus name comes from the Greek *phakelos*, meaning fascicle, and referring to the congested inflorescences (Hitchcock and Cronquist, 1973).

Phacelia capitata is a member of the species group *Magellanicae*, in the subgenus *Phacelia*. The *Magellanicae* comprises the well-known *P. magellanica* polyploid complex

(Figure 1). This complex was intensively studied by Heckard (1960) after cytological studies (Cave and Constance, 1942, 1944, 1947, 1950, 1959; Heckard, 1956; Kruckeberg, 1956) that revealed the existence of polyploidy among its members. Superimposed on a series of six diploid (n=11) species is an interfertile complex of tetraploids (n=22) and a few hexaploids (n=33). At the time of his study, Heckard (1960) stated that each of the basic diploid species, except P. capitata, has a "...morphologically similar counterpart on the tetraploid level which intimately associates it with the superstructure of intergrading tetraploids." This intergradation between polymorphic tetraploid species, often accompanied by introgression (Anderson, 1949), has led to very complex, and sometimes indecipherable, patterns of variation. Heckard (1960) summarized the problem:

> For the most part, as is characteristic of introgressing taxa, entire series of populations, which sometimes extend throughout large areas, are involved in the genic recombinations, resulting in a variation pattern that is extremely difficult to analyze. This is especially true in this complex where the initial differences are not of a magnitude to furnish characters which can be conveniently measured. The result of this intergradation is an extensive assemblage of interrelated plants within which lines must be drawn somewhat arbitrarily in order to delimit taxonomic units.

As a result of such variation patterns, the Magellanicae has had a protracted taxonomic history. At one time or another, the complex has been said to include five or more species, and as few as three species. In his final

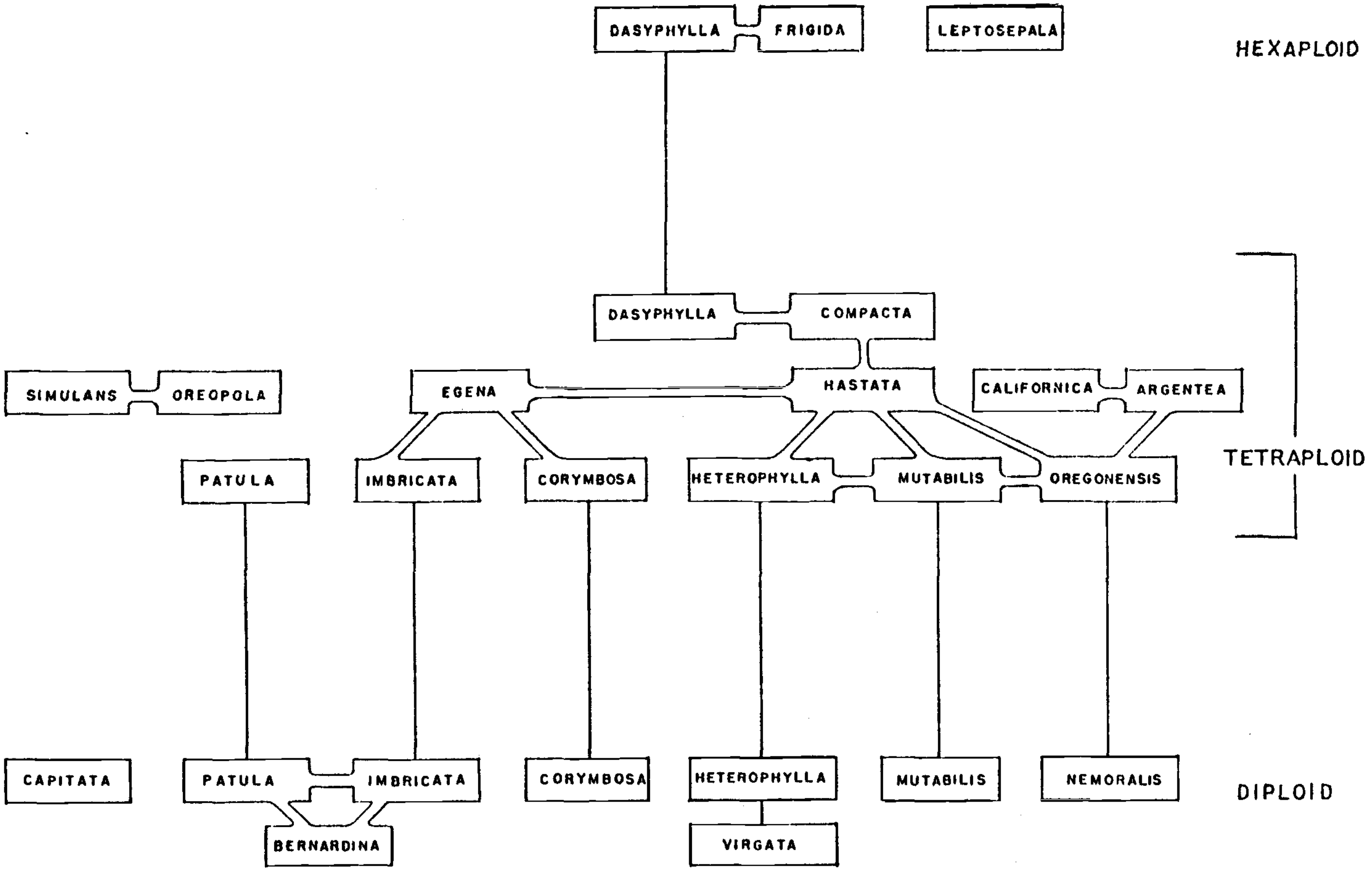


Figure 1. The Phacelia magellanica polyploid complex (species group Magellanicae). From Heckard (1960).

taxonomic treatment, Heckard (1960) recognized 13 species in the United States and Canada.

The first collection of a *P. capitata*-like plant was made on June 22, 1916 by Peck (*6022*, WILLU), from a "(d)ry slope near Roseburg, Douglas Co." It was subsequently annotated at the Gray Herbarium, in 1919, as "*Phacelia californica* forma *egena*." In his description of *P. capitata*, Kruckeberg (1956) mentioned the resemblance of this specimen to the new species, but he assigned no name to it. Although the silvery, entire leaves of this plant are suggestive of *P. capitata*, it lacks the inflorescence features of the species. The possible interrelationships of *P. capitata* with this, and other problematic specimens from the Roseburg-Myrtle Creek area, will be discussed in the final section of this thesis.

Other collections made in 1916 by Peck (*6033*, "(d)ry bank, Roseburg, Douglas Co.", and *6035*, "Reston, Douglas Co.", both WILLU), were also discussed by Kruckeberg (1956) in relation to *P. capitata*. However, these two specimens seem to best fit the description of *P. hastata* offered by Heckard (1960). The Reston vicinity was searched during my study, but only individuals of *P. hastata* were located.

The first collection of "pure" *P. capitata* was made on April 13, 1934, "2 miles south of Myrtle Creek, Douglas Co., Oregon," by Eastwood and Howell (*1474*, CAS). This specimen went unidentified until it was annotated as *P. capitata* Kruckeberg *in ed*. in 1955, by both Heckard and

Kruckeberg. On the same date as the above collection, Eastwood and Howell obtained another specimen (*1475*, CAS) from "Myrtle Creek, Douglas Co., Oregon," which they originally labeled *P. leucophylla*. Once again, Kruckeberg acknowledged its resemblance to *P. capitata* but did not name it as such. Heckard annotated it in 1960 as *P. capitata*, "(p)ossibly a tetraploid form?" I was unable to relocate similar specimens in the field. A hybrid origin for such a plant is possible.

The next "good" collection was made in 1939 by Peck (*20324*, UC), presumably from the eventual type locality, a "stony slope near Bridge, Coos Co." This specimen also went unidentified until it was annotated by Kruckeberg as *P. capitata in ed*. in 1954, and he eventually designated it as a topotype.

A specimen collected by Constance and Rollins (*2956*, DS) in 1942, from Mt. Nebo near Roseburg, was originally labeled *P. leucophylla*. Like *Eastwood and Howell 1475*, this collection was acknowledged as morphologically reminiscent of *P. capitata* by Kruckeberg, but again he did not recognize it as such. It was annotated in 1961 as *P. capitata* by Heckard, and although it was a tetraploid, he commented (pers. comm.) that the plant may combine genotypes of *P. capitata* and *P. corymbosa*. I was unable to locate individuals similar to this in the field, the plants found on Mt. Nebo being most readily referable to *P. hastata*.

The next collections of P. capitata were made in Douglas County by Detling, first in 1942 from Red Mountain (5314, ORE), and then in 1949 from Nickel Mountain (6339, ORE). These specimens were also originally labeled as P. leucophylla, until being annotated as P. capitata by Kruckeberg in 1961.

The holotype collection of P. capitata was made in 1951 (Kruckeberg 2703, WTU), from a "serpentine roadcut, 2 miles east of Bridge, above Coquille River and along State Highway 42, Coos County, Oregon." It was described and illustrated five years later (Kruckeberg, 1956). Since 1951, P. capitata has been sporadically collected on serpentine outcrops in south-central Douglas and northwestern Jackson Counties, as well as being re-collected from the type locality in Coos County.

In his description of the species, Kruckeberg (1956) compared it to two close relatives, P. corymbosa and P. leucophylla. However, P. leucophylla was placed in synonymy under P. hastata by Heckard (1960). Further comparisons of P. capitata with P. corymbosa, P. hastata, and one other member of the complex, P. heterophylla, are made in a later section on the morphology of the species, and a description of P. capitata is presented.

In his studies, Heckard (1960) emphasized the California members of the Magellanicae. Consequently, he made "(n)o attempt...to depict the interrelationships within the complex of Phacelia capitata Kruckeberg..." The goals of my study were to consider certain aspects of the biosystematics, ecology, and distribution of P. capitata, in order to ascertain, to the extent possible, its relationships within the species group Magellanicae. It is hoped that the study will contribute to a better understanding of this complex group.

ENVIRONMENTAL RELATIONSHIPS

Geology

The geology of the Klamath Mountains in southwestern Oregon and northwestern California is extremely complex and poorly understood. Some of the oldest rocks in Oregon are found in the Klamath Mountains, near the Oregon-California border. The age of these highly metamorphosed rocks is thought to be at least 425 million years (Alt and Hyndman, 1978). This section presents a review of the terminology of serpentine substrates, an outline of the Klamath Mountains province, and a brief summary of the current theories as to how the serpentine areas became emplaced.

Traditionally, the word "serpentine" has been used to define all ultramafic rocks and the soils weathering from them. The term "ultramafic" encompasses all those rock types in which the elemental composition largely consists of silicates of iron and magnesium, derived from the mineral olivine. The most common ultramafics are the igneous rocks peridotite and dunite, and their metamorphic derivative, serpentinite (Kruckeberg, 1969).

The Klamath Mountains, of which the Siskiyou Mountains along the Oregon-California state line are a part, are bordered on the north by the Oregon Coast Range, on the south by the California Coast Range, and on the east by a portion of the Cascade Range. The northern contact with the Oregon Coast Range extends along a line southwest of the Bandon area, to the Rogue River, and then northeast to the Roseburg vicinity. The contact with younger volcanic rocks of the Cascades runs south from the Roseburg area to Medford, southeast over the mountains near Siskiyou Pass, to Redding, California. The southern border of the Klamath Mountains then traverses southwest, thence northwest, almost to the California-Oregon state line (McKee,1972).

The ultramafic outcrops occupied by _Phacelia capitata_ (and _P. corymbosa_ in Oregon) are scattered throughout Curry, Josephine, Jackson, Coos, and Douglas Counties (Figure 2). The most extensive, contiguous outcrops are found in southern Curry and Josephine Counties (i.e., the Josephine Peridotite sheet). To the north of these expansive outcrops, the ultramafic areas become more widely distributed, smaller in size, and separated by wider areas of non-ultramafic substrates. There is an overall southwest-northeast trend in the alignment of the outcrops.

The geology of the Klamath Mountains, and indeed all of Oregon, is the result of a prolonged collision between the North American continent and the Pacific Ocean floor which began about 200 million years ago (early Mesozoic Era), and continues today. Muddy sediments on the ocean floor rest on basalt lava flows, which in turn rest on serpentinite, a green rock that forms when heavier rocks beneath it absorb water. These heavier serpentinite precursors are peridotite. As the seafloor slides under the continental margin, the muddy sediments, and

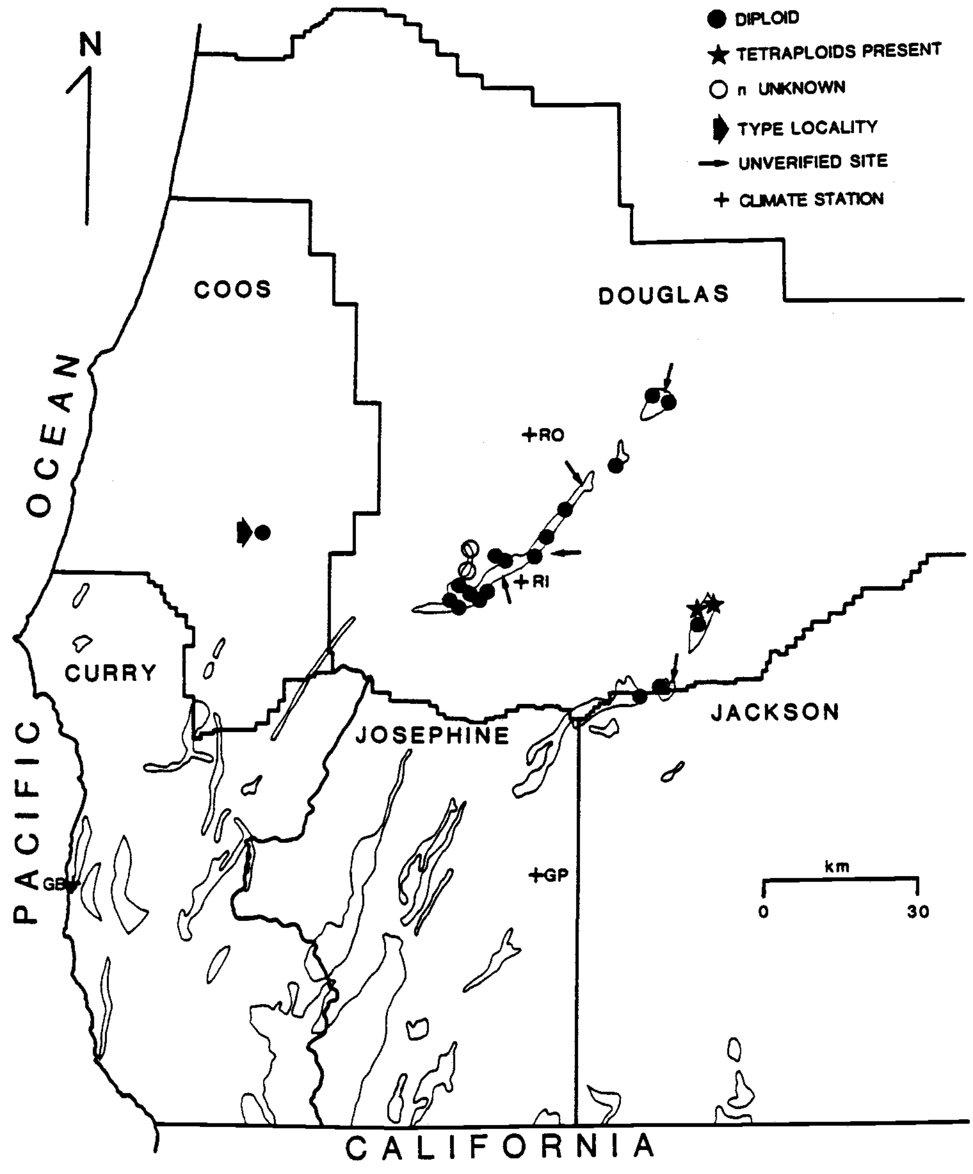


Figure 2. Distribution of *Phacelia capitata* in southwestern Oregon. Ultramafic formations outlined (Wells and Peck, 1961).

occasionally slabs of bedrock seafloor containing peridotite and serpentinite, are added to growing coastal ranges such as the ancient Klamath Mountains. When such a slab is pressed against the continental margin, the ultramafic rocks can be squeezed through fault zones in the accumulating mass (Alt and Hyndman, 1978). Serpentinite is so soft and easily deformed that it can be pressed up cold along faults. Under pressure, it takes on the "consistency of toothpaste" (McKee, 1972). The intrusion of many ultramafic bodies in southwestern Oregon occurred during the Jurassic Period, between 190 and 136 million years ago. However, they may be remobilized with further compression, and some bodies may have been moved to their present location as recently as the Eocene Epoch, approximately 30-38 million years ago (Baldwin, 1976).

Soils

The effects of serpentine soils on the physiognomy and composition of vegetation have been related to various physical and chemical properties of such substrates. A review of the properties of these soils, and the results of soil sample analyses, are presented in order to characterize the edaphic environments of P. capitata, and the more southerly serpentine species, P. corymbosa.

Understanding the influence of serpentine soils on vegetation has been problematic in the past, because of numerous attempts to find one single property of these soils which universally explains their unique impact on plant life. In the words of Proctor and Woodell (1975), "(t)his has led to unnecessary controversy, for serpentines are exceedingly variable." This variability defeats efforts to generalize about the serpentine phenomenon.

Physically, serpentine soils vary from exceedingly rocky (i.e., lithosols), to having a high clay and organic matter content (i.e., azonal soils)(Walker, 1954; Proctor and Woodell, 1975). Undesirable physical characteristics (i.e., shallow soil mantle, gravelly texture, low clay content, and steep topography) can result in reduced moisture and nutrient levels (Walker, 1954). However, these conditions may exist in soils of diverse parent materials. The conclusion has been that, while physical properties should be considered as part of the complex of factors making serpentine soils unfavorable for plant growth, they are rarely of overriding importance; soil chemistry provides the discriminating influence (Walker, 1954; Kruckeberg, 1969; Proctor and Woodell, 1975). It is interesting to note that, while serpentine soils have often been equated with xeric soil conditions, Whittaker (1960) found no significant differences in soil moisture between serpentine and non-serpentine soils in measurements from the Siskiyou Mountains.

Proctor and Woodell (1975) evaluated at length the chemical characteristics most often cited as the causes for serpentine soil infertility and toxicity. These have included low levels of the major nutrients nitrogen, phosphorous, and potassium; high levels of heavy metals, especially nickel, chromium, and cobalt; and frequently, low levels of calcium coupled with high levels of magnesium.

The effects of major nutrient levels on plant growth vary with the species under consideration. In some cases, addition of N, P, and K to serpentine soil leads to an increase in plant growth, while in others no improvement is seen (Proctor and Woodell, 1975). These differences in response are one of the best demonstrations of the variability of serpentine soils and of plant responses to them. Proctor and Woodell claim that few workers would now subscribe to the view that low major nutrient levels largely account for the chemical stringency of serpentine soils. One example in which nutrient addition increased plant growth is detailed by Turitzin (1982), in a study of nutrient limitations on a serpentine area in California. In assessing the effects of adding nutrients to the soil on the growth of two annual grasses (_Bromus_ _mollis_ and _Vulpia microstachys_), it was found that nitrogen and phosphorous were the limiting nutrients, while added calcium had no effect on the productivity of these species. As mentioned, however, possible variability in the responses of other species in a given area should be kept in mind.

A large body of literature has developed regarding the biological effects of high concentrations of heavy metals which frequently characterize serpentine soils. Again the situation is very complex, and soils from different sites are highly variable in their heavy metal content. Variability in the ecological significance of heavy metals is due to several factors, including diversity of parent rock origin and weathering, other soil characteristics (i.e., pH and redox potential), lower uptake of organic metal compounds, modification of metal toxicity by the presence of other elements, and variability (both inter- and intraspecific) in the response of plants to heavy metals (Proctor and Woodell, 1975). In summarizing the research on the effects of nickel, chromium, and cobalt on plant growth, Proctor and Woodell conclude that, 1) there is good evidence for many serpentine soils and plants that nickel is an important factor, and equally good evidence in other cases that it is of little or no importance; 2) the same considerations about variability apply to chromium as to nickel, but there is generally less evidence that chromium is important in serpentine soils; and 3) there is frequently little evidence for cobalt being as important as nickel or chromium in such soils.

The status of calcium and magnesium in serpentine soils has also been of major interest in assessing their infertility. A low Ca/Mg ratio (i.e., less than 1.0) has often been cited as the most important adverse characteristic influencing plant growth; in other cases, low Ca levels alone are emphasized, and in yet others, high

Mg (Proctor and Woodell, 1975). In any event, these authors are of the opinion that both Ca and Mg should have major consideration in any account of serpentine soil infertility.

The results of White (1971) adequately demonstrate the complexity of the serpentine soil phenomenon. He conducted a detailed series of soil-chemical and vegetation analyses in serpentine and non-serpentine contact areas of southwestern Oregon. No substantiation was found for the "low Ca theory" which had earlier been espoused by Walker (1954) and Kruckeberg (1954). In some areas, the highest Ca levels occurred on serpentine soils. It was also found that a low Ca/Mg ratio alone could not explain the vegetation discontinuities observed. White found that distributions of individual species within the study transects were principally influenced by concentrations of Mg, Ni, and Cr, in that order. He concludes that earlier explanations of serpentine infertility based on low Ca/Mg ratio, high Fe, and low Ca should be modified to incorporate the predominant influence of consistently high levels of Mg, Ni, and Cr. As emphasized earlier, however, even these results are perhaps best restricted to interpretations of plant distributions in the area studied.

The overall importance of high levels of magnesium is also acknowledged by Proctor and Woodell (1975). They cite the observations that, 1) many serpentine-endemic plant species have a requirement for high amounts of this element for optimum growth, and 2) the levels of magnesium in serpentine soils have been shown to be toxic to many non-serpentine species. In their words, a "high magnesium requirement might be of more general importance in explaining the restriction of some plants to serpentines."

The most reasonable conclusion is that the stringency of serpentine soils is correlated not with any single chemical or physical property of such soils in general, but with a suite of factors, mainly chemical in nature. These factors may vary depending on the composition and age of the parent rocks, topography, climate, and the biota of any given area. Chemical factors may vary, as well, in the extent of their interactions with each other (Proctor and Woodell, 1975).

Table 1 presents the results of analyses of eight soil samples conducted by the Soil Testing Laboratory at Oregon State University. The extraction and analysis methods are outlined by Berg and Gardner (1978). Soils at the Boomer Hill I site (P. capitata and P. hastata) appear to be derived from metamorphic rocks that are similar to serpentine but are darker blackish-orange in color. The Tiller sample is from a non-serpentine area adjacent to the serpentine outcrops along Elk Creek. The remaining six samples are all soils derived from fully serpentinized parent materials.

The serpentine soils are all characterized by low levels of phosphorus and low Ca/Mg ratios. The sub-

Table 1. Selected soil analyses for eight *Phacelia* sites in southwestern Oregon.

Species and population	Soil type	pH	P (ppm)	K (ppm)	Ca meq/100g	Mg meq/100g	Ca/Mg ratio	Cu (ppm)	Fe (ppm)	% Organic matter
P. capitata										
Beatty Creek	serpentine	7.1	4	35	2.1	12.3	0.17	1.1	74	4.7
Boomer Hill I	sub-serpentine	6.2	19	82	17.6	7.7	2.3	1.8	124	5.4
Bridge	serpentine	6.9	2	140	3.1	20.0	0.16	2.1	64	4.0
Elk Creek	serpentine	7.5	1	70	1.7	20.4	0.08	2.4	84	1.9
Peel	serpentine	6.7	4	31	1.7	10.4	0.16	0.76	86	5.0
P. corymbosa										
Eight Dollar Mtn II	serpentine	6.9	1	39	2.5	23.3	0.11	1.7	94	3.3
Grave Creek	serpentine	7.2	1	39	2.0	11.5	0.17	1.1	40	2.6
P. heterophylla										
Elk Creek	non-serpentine	6.8	34	43	6.3	1.2	5.25	1.5	142	2.4

serpentine sample has a higher Ca/Mg ratio than the more typical serpentine soils, but it is within the range of values reported by Proctor and Woodell (1975) for such soils.

Although large amounts of iron are often found in serpentine soils (Proctor and Woodell, 1975), the results do not indicate this for the samples used in this study. The highest concentrations of iron are found in the sub-serpentine and non-serpentine samples.

The remaining analyses (pH, K, Cu, and organic matter) do not indicate any consistent differences between the serpentine samples and the non-serpentine sample. Serpentine soils from the *P. capitata* and *P. corymbosa* sites are quite similar in chemical composition.

Climate

The climate of western Oregon, west of the Cascade Mountains, is maritime, being influenced by the moderating effects of the Pacific Ocean. The mountain barrier of the Cascades largely prevents any continental influence in the western portion of the state.

Along the coast, the climate is quite equable. Annual temperatures range from a minimum of approximately 2 ° C, to a maximum of approximately 20°C. Rainfall in this belt ranges from 1270 mm to 2540 mm, depending on the elevation of the Coast Range and the nearness of the mountains to the ocean. Freezing weather and snow are rare.

Inland from the coast, there is a general decline in precipitation amounts, and temperatures show a greater annual variation. These trends are influenced by higher elevations in certain areas.

The inland regions of southwestern Oregon, between the Coast and Cascade Ranges, have a climate which is generally characterized by mild winters and by summers in which days may be quite warm and nights moderately cool. In January, the normal minimum temperature is approximately -1 ° C; in July, normal maximum temperatures range from 28 ° C to 33 ° C, with extremes of 38°C not uncommon. Normal annual precipitation in the valleys ranges from 305 mm to 940 mm; in the mountains the amounts are greater. Some snowfall occurs each winter; in the valleys the average annual amount ranges from 178 mm to 483 mm, again with considerably more in the mountains (U.S.D.A. Weather Bureau, 1930).

Climatic data for selected weather stations in southwestern Oregon are summarized in Table 2. The locations of these stations are indicated in Figure 2.

Site locations and characteristics

Methods. A compilation of 13 known locations for Phacelia capitata was made from herbarium collections at Oregon State University (OSC), and from the Oregon Rare, Threatened, and Endangered Plant files housed there.

Table 2. Climatic data for selected weather stations in southwestern Oregon, 1951-80 (National Oceanic and Atmospheric Administration, 1982).

Station Name & Elev. (m)	Temperature Averages (°C)						Precipitation Averages (mm)		
	January	July	Daily Maximum		Daily Minimum		Annual	January	July
			January	July	January	July			
Gold Beach 15	8.3	15.0	12.1	19.6	4.6	10.4	2099.8	369.3	9.3
Grants Pass 282	4.4	22.0	8.3	32.4	0.4	11.5	820.7	164.1	5.3
Riddle 202	5.0	20.1	8.9	28.9	1.1	11.3	802.9	151.1	4.1
Roseburg 142	5.1	20.2	9.1	29.0	1.1	11.4	847.1	151.4	4.8

Location information was also obtained from two Bureau of Land Management botanists, Mr. Russ Holmes, Roseburg, and Ms. Joan Seevers, Medford, Oregon.

Field studies were conducted during May-July 1982, April 1983, and April-June 1984. During initial field surveys, as many locations as possible, in both serpentine and non-serpentine areas of southwestern Oregon, were surveyed to determine the location and status of *P. capitata* populations.

Results. Of the 22 verified populations of *P. capitata* which were intensively studied (Table 3), 17 sites were relocations of previously observed localities. Five new locations for the species were found (Boomer Hill I, Cow Creek I and II, Doe Creek, and The Drew).

Five previously reported sites for *P. capitata* were not located or studied during the course of this project (Table 3). Two of these (Brushy Butte and Nickel Mountain) were inaccessible due to restrictions on entering private land; the latter location is the site of the Hanna Nickel Corporation mine. In both of these cases, *P. capitata* is likely to be present, since suitable habitat is visible from surrounding areas. The Rattlesnake Creek site is part of an extensive population system which is located along the Little River near the town of Peel. Individuals of *P. capitata* can be seen along many portions of the Little River Road in this area, and the two sites selected for study (Little River and

Table 3. Reported locations of *Phacelia capitata* in Oregon. All locations are in Douglas County except Goolaway Gap (Jackson County) and Bridge (Coos County).

Site	Population number (CLUSTER)	T	R	Sec	Location	Elev. (m)	Aspect	Slope %	Years	Ownership
A. VERIFIED LOCATIONS										
Beatty Creek	A090	30S	6W	31	0.4 km N of Cow Creek Rd Beatty Creek RNA	320	E,SE,W	55-65	1979 Dwan & Balk 1982-4 Shelly	BLM & private
Bilger Creek	A050	29S	5W	3	BLM rd 29-5-11.0, 2.3 km NW of Bilger Creek Rd	490	S	50	1982 Holmes 1983-4 Shelly	BLM & private
Boomer Hill I	A080	30S	6W	5	BLM rd 30-6-4.2, 8.1 km SW of Interstate Hwy 5 on Boomer Hill Rd.	760	WSW	35	1983-4 Shelly	BLM
Boomer Hill II	-	30S	6W	9	BLM rd 30-6-4.1, 0.5 km from BLM rd 29-6-34.0	850	ESE	40	1978 Crowder 1984 Shelly & Holmes	BLM
Bridge	A210	29S	11W	35	N of St Hwy 42, 3.2 km E of Bridge	100	S	50	1951 Kruckeberg 1980 Sundberg 1982-4 Shelly	private
Callahan Creek	A180	31S	2W	9	Umpqua NF rd 3230, 0.5 km W of St Hwy 227	490	SE	75	1979 Fosback 1983-4 Shelly	private & USFS
Cow Creek I	A120	30S	7W	35	Cow Ck Rd, 0.5 km W of Doe Ck Rd	300	WNW	65	1983-4 Shelly	BLM
Cow Creek II	A130	30S	7W	34	NW side of Cow Creek, 1.2 km SW of Doe Ck Rd	300	SE	60	1983-4 Shelly	private
Cow Creek Turn-off	A160	30S	7W	36	Cow Ck Rd, 4.8 km W of Glenbrook Loop Rd	230	S	5	1979 Dwan & Balk 1984 Shelly	private
Doe Creek	A15A	30S	7W	22	Doe Ck Rd, 1.9 km N of Cow Ck Rd	400	-	0	1984 Shelly	private

Table 3. Continued.

Site	Population number (CLUSTER)	T	R	Sec	Location	Elev. (m)	Aspect	Slope %	Years	Ownership
Doe/Thompson Ridge	A150	30S	7W	14	BLM rd 30-7-14.0, 3.2 km NW of Doe Ck Rd	640	ESE,SE	40	1982 Holmes 1982 Shelly & Holmes	private
The Drew	A190	31S	2W	21	Umpqua NF rd 3130E, 3.1 km from NF rd 3130	810	ESE	25	1982-4 Shelly	private
Elk Creek	A170	30S 31S	2W 2W	34 3	St Hwy 227, 1.6-4.0 km SE of Tiller	375	W,WSW	60-80	1972 Heckard 1979 Fosback 1983-4 Shelly	private, BLM, USFS
Goolaway Gap	-	32S	3W	31 32	0-0.8 km W of Goolaway Gap	930	E,SE	20-30	1981 Seevers 1982-4 Shelly	BLM & USFS
Lee Creek	A030	28S	4W	15	BLM rd 28-4-15.0, 0.5 km NW of Lee Ck Rd	415	S,E	0-70	1977 Fosback 1982-4 Shelly	BLM
Little River	A010	26S	3W	28	Co Rt 17, 5.9 km SE of Glide	270	SE	35	1976 A & F Parker 1982-4 Shelly	private
Myrtle Creek North	A060	29S	5W	20	Co Rt 14, 1.6 km N of St Hwy 99, NW of Myrtle Ck	245	SSE	70	1952 Howell 1983-4 Shelly	private
Peel	A020	26S	3W	35	BLM rd 26-3-34.2, 0.5 km E of Peel	295	S	25	1977 Knouse & Moore 1982-4 Shelly	private
Red Mountain	-	32S	3W	27	SW flank of Red Mtn, 0.8 km N of Jackson-Douglas County line	930	E,SE	0-20	1942 Detling 1984 Shelly & Nelson	USFS
Rice Creek	A070	29S	7W	35	BLM rd 29-7-36.0, 1.2 km W of Rice Ck Rd	710	ESE	20-30	1978 Crowder 1984 Shelly & Holmes	private
Salt Creek	A140	30S	7W	36	BLM rd 30-7-36.0, 0.5 km NE of Cow Ck Rd	340	S	15	1982 Holmes 1984 Shelly & Nelson	private
Weaver Road	A06A	29S	5W	40	Weaver Rd, 2.9 km SW of Interstate Hwy 5	210	SE	55	1966 Ornduff 1984 Shelly	private

Table 3. Continued.

Site	Population number (CLUSTER)	T	R	Sec	Location	Elev. (m)	Aspect	Slope %	Years	Ownership
B. UNVERIFIED LOCATIONS										
Brushy Butte	-	28S	4W	18	Ca 9 km S of Dixonville	610	N,NW	?	1979 Miles	private, BLM?
Myrtle Creek South	-	29S?	5W	?	"2 mi S of Myrtle Creek"	180?	?	?	1934 Eastwood & Howell	private?
Nickel Mountain	-	30S	6W	21	Nickel Mountain, ca 6.5 km W of Riddle	365?	SE?	?	1949 Detling	private
Rattlesnake Creek	-	26S	3W	34	Little River Rd, 8 km from St Hwy 138	320	S,SW	50	1982 Holmes	private
Red Mt Lookout	-	32S	3W	23	Red Mt lookout, and N along ridgetop	1460	?	?	1983 Norris	USFS

Peel) are on each end of this series of populations. I was not aware of the Red Mountain Lookout site until after the 1984 field season. The historical collection by Eastwood and Howell (_1474_, CAS) is labeled as being "2 miles S. of Myrtle Creek, Douglas County." This vicinity was surveyed, but no plants were located.

The entire known geographic range of _Phacelia capitata_ occurs in south-central and western Douglas, southern Coos, and northwestern Jackson Counties, in southwestern Oregon (Figure 2). The northernmost location for the species occurs along the Little River in Douglas County. The southernmost location is near Goolaway Gap, southeast of Cedar Springs Mountain, in Jackson County. The westernmost location is the most isolated of the 22 sites studied and is also the type locality (Kruckeberg, 1956); this site is near Bridge, in Coos County. The easternmost location is along Elk Creek, just southeast of Tiller in Douglas County.

The serpentine outcrops where _P. capitata_ is found are the northeasternmost such substrates in southwestern Oregon (Figure 2). In general, the sites studied are located on slopes with southerly exposures; a few are in level areas, or on slopes with west, northwest, or east exposures. The steepness of these sites is quite varied, with slopes ranging from 0 to 80%. The lowest elevation at which _P. capitata_ occurs is at the type locality near Bridge, where a portion of the site is at approximately

100 m. The highest elevation study site is 930 m at Goolaway Gap, although the unverified Red Mountain Lookout site, 7.1 km northeast of Goolaway Gap, apparently occurs at an elevation of 1460 m.

It is of great interest to field inventory studies of P. capitata that the species shows a strong favorable response to disturbance at many locations. The ecological and evolutionary ramifications of this will be discussed in a later section. It is sufficient here to state that, at 18 of the 22 sites studied, the serpentine habitats have been at least partially disturbed, mainly by quarrying activities and construction of roads and railroads. Only at the Beatty Creek, Bridge, Red Mountain, and Rice Creek sites are the habitats largely or completely undisturbed; there is some light grazing by livestock at the Bridge site. Phacelia capitata increases in abundance so greatly in disturbed areas, that many of its populations have been "released" from any paucity that may have characterized them in earlier times. This weedy tendency is shared with most of the other taxa of the species group Magellanicae (Heckard, 1960).

To the south of its range, P. capitata is replaced on serpentine soils by the closely related species P. corymbosa. The latter species, in addition to occurring in the Siskiyou Mountains region of Oregon and California, grows in the north Coast Ranges of California and in one location in Butte County, California, in the Sierra

Nevada. The geographic ranges of these two species approach most closely in northwestern Jackson County, Oregon, in the area southwest of Cedar Springs Mountain. Here, the Goolaway Gap site for P. capitata occurs along a 0.8 km stretch of the West Fork Evans Creek Road, west of the gap. Phacelia corymbosa is found approximately 8.9 km to the southwest, along Grave Creek. These two locations are separated by an area of non-serpentine substrates. Nowhere were these two species found in biotic sympatry (see Figure 8, page 104). The Grave Creek location for P. corymbosa represents one of the two northernmost known locations for this species; the other is on Iron Mountain, in southern Coos and northern Curry Counties (Baker, 1956).

Associated vegetation

The spectacular influences that ultramafic substrates have on the plant life which inhabits them has been of great interest to both community ecologists and biosystematists. These effects are of physiognomic and taxonomic importance. Serpentine vegetation is frequently dwarfed, and xerophytism is common. Species composition is often unique, and endemism and range disjunction are characteristic of serpentine floras (Kruckeberg, 1969). In the words of Whittaker (1954), most serpentine vegetations throughout the world appear to be dominated by some one, or some combination, of three growth forms:

coniferous trees, sclerophyllous shrubs, and "grass-like plants." He states that the stunted, open appearance of Siskiyou serpentine vegetation results from the reduction in size and numbers of *Pseudotsuga menziesii* and the exclusion or reduction to shrubby equivalents of the broad-leaved trees. In soils of less favorable nutrient status such as serpentines, there is a trend towards opening, lowering, and reduction of the plant community toward the lower strata (Whittaker, 1954).

The plant associations occurring on ultramafic soils in the Siskiyou Mountains have been studied by Whittaker (1954, 1960), White (1971), and Atzet and Wheeler (1984). In his gradient analysis studies, Whittaker found that, on a gradient from more mesic, low elevation sites to more xeric, higher elevation sites, the vegetation changes from fairly open *Chamaecyparis lawsoniana*-*Pinus monticola*-*Pseudotsuga menziesii* stands, through distinctive intermediate forest-shrub stands of *Pseudotsuga*-*Pinus monticola*-*P. lambertiana*-*P. jeffreyi*-*Calocedrus decurrens*, to very open stands of *P. jeffreyi* and occasional *C. decurrens*. This latter community is termed a woodland, "temperate savannah," or pine steppe (Whittaker, 1954).

White (1971) observed five plant associations on serpentine substrates in southwestern Oregon, their characteristics being related to elevation and successional status. Gentle, rocky slopes above 1200 m are distinguished by the open character of the vegetation.

Important species include *Festuca idahoensis*, *Poa sandbergii*, *Allium falcifolium*, *Aspidotis densa*, and *Ceanothus cuneatus*. At middle elevations (860-980 m) the vegetation retains its open character, but shrubby species, including *Ceanothus cuneatus*, increase in abundance.

Below 860 m, the vegetation transects were grouped according to successional status, i.e., young, intermediate, or climax. Within the youngest successional areas, annual species are predominant (*Epilobium minutum*, *Vulpia microstachys*, *Aira caryophyllea*, *Agoseris heterophylla*, *Githopsis speculariodes*, and *Madia exigua*). These species are considered to be indicators of open mineral soils.

In the successionally intermediate areas, *Ceanothus cuneatus* becomes important, along with an increase in perennial grasses and forbs (*Stipa lemmonii* and *Eriophyllum lanatum*) and the fern species *Aspidotis densa*.

The climax community at elevations below 860 m is described as an open grassland savannah with scattered *Pinus jeffreyi* and occasional *Calocedrus decurrens*. There was a notable absence of *Ceanothus cuneatus*. The herbaceous stratum is dominated by perennial grasses (*Stipa lemmonii*, *Danthonia californica*, *Koeleria nitida*, and *Festuca* spp.) and forbs (*Ranunculus occidentalis*, *Monardella villosa*, *Polygala californica*, and *Achillea lanulosa*). Notable in the climax situation was the absence of *Aspidotis densa*. There was a low abundance of species indicative of open mineral soil, due to the limited amount of such habitat (White, 1971).

Atzet and Wheeler (1984) further described the *Pinus jeffreyi* Series in the Siskiyou Mountains. The *P. jeffreyi*/grass Association is defined as occurring below approximately 1390 m. The climax dominant is *P. jeffreyi*, with approximately 55% average cover of herb and grass species.

Vegetation sampling. Quantitative data were collected in order to describe the associated species and plant community type with which *Phacelia capitata* generally occurs. This study was conducted within, and adjacent to, the Beatty Creek Research Natural Area (RNA; see Table 3). The site is located approximately in the center of the known geographical range of the species, and the plant community is undisturbed.

Methods. The data were collected in five 1000 m^2 circular macroplots. Two macroplots were situated on an east-facing slope along the west side of Beatty Creek, within the RNA. The other macroplots were located on the west-facing slope above the east side of the creek, outside the RNA.

Within each macroplot the following data were collected: m^2 canopy coverage of tree and shrub species, and for *Pinus jeffreyi* and *Pseudotsuga menziesii*, the number of trees greater than 3 m in height and the number of trees less than or equal to 3 m in height. The slope and aspect of each macroplot were also noted. The average elevation of the area is approximately 320 m.

Within each macroplot were placed eight 0.25 m^2 microplots (40 total), 2 on each of 4 radii. The radii were positioned at 90° angles to each other, and at 45° angles to the up-downhill axis of each macroplot. On each radius, the microplots were placed on the uphill side, 6 and 12 m from the center of the macroplot.

Within each microplot, all species of herbaceous plants present were listed. Approximate canopy coverage of each species was then recorded, according to the canopy coverage classes of Daubenmire (1959):

Cover class	% canopy coverage	Midpoint %
1	0-5	2.5
2	5-25	15.0
3	25-50	37.5
4	50-75	62.5
5	75-95	85.0
6	95-100	97.5

Results. The sampling results for the associated trees and shrubs are given in Table 4. The results for the herbaceous vegetation are given in Table 5.

The plant community with which *P. capitata* is associated at Beatty Creek is dominated by *Pinus jeffreyi* in the tree layer. Individuals of the latter are scattered, giving the community the well-documented "savanna" appearance. Notable shrubs include *Ceanothus cuneatus* and *Rhus diversiloba*.

Thirty-six herbaceous species were encountered in the

Table 4. Associated tree and shrub vegetation at Beatty Creek. Data were collected in five 1000 m^2 circular plots, and are presented as percent canopy cover; for Pinus jeffreyi and Pseudotsuga menziesii, figures in parentheses indicate the number of stems greater than 3 m, and the number less than or equal to 3 m, in height. Study dates: 25-26 April 1984.

Plot	1*	2*	3	4	5
Slope position	low	low	low	middle	high
Slope (%)	56	63	60	50	49
Aspect	E	SE	W	WSW	SW
Trees					
Pinus jeffreyi	30(18;6)	15(18;19)	7.5(10;6)	7.5(18;7)	30(30;35)
Pseudotsuga menziesii	1.6(1;0)	2.0(1;0)	0	0	0.15(0;1)
Umbellularia californica	0	3.5	0.25	0	0.4
Arbutus menziesii	0	1.8	2.5	0	0
Shrubs					
Ceanothus cuneatus	0.1	1.1	0	0.05	0.05
Holodiscus discolor	1.8	0	0	0	0
Rhus diversiloba	0.15	0.6	0.05	0	0.15

*-Plots located within the Beatty Creek Research Natural Area.

Table 5. Herbaceous vegetation at Beatty Creek. Data are averages of percent cover (using canopy cover class midpoints), and percent frequency, in 40 0.25 m^2 plots; study dates: 25-26 April 1984.

Species	Average % cover	% Frequency
Grasses and graminoids		
Bromus carinatus	1.0	15.0
Luzula campestris	6.5	40.0
Melica geyeri	0.1	5.0
Poa scabrella	16.3	45.0
Vulpia microstachys	1.5	47.5
Annual forbs		
Collinsia parviflora	0.9	37.5
Cryptantha intermedia	1.1	42.5
Crocidium multicaule	0.1	5.0
Galium aparine	0.9	37.5
Githopsis specularioides	0.1	5.0
Plectritis congesta	0.6	10.0
Thysanocarpus curvipes	0.1	5.0
Perennial forbs (including ferns)		
Achillea millefolium	0.4	2.5
Aspidotis densa	12.6	82.5
Brodiaea pulchella	0.2	7.5
Castilleja pruinosa	0.4	15.0
Cerastium arvense	0.9	10.0
Delphinium menziesii	0.1	5.0
Dodecatheon hendersonii	0.1	5.0
Eriophyllum lanatum	1.1	32.5
Eriogonum nudum	0.5	20.0
Erythronium oregonum	0.7	27.5
Hieracium scouleri	6.5	35.0
Iris chrysophylla	6.4	20.0
Lithophragma parviflora	0.4	15.0
Lomatium nudicaule	1.6	27.5
Lupinus albifrons	0.1	5.0
Microseris sp.	0.1	5.0
Monardella villosa	2.3	43.5
Phacelia capitata	0.4	2.5
Ranunculus occidentalis	2.9	40.0
Saxifraga occidentalis	0.1	5.0
Sedum sp.	0.5	20.0
Silene hookeri	1.9	50.0
Thlaspi montanum var. montanum	3.8	77.5
Viola hallii	0.1	5.0

microplots. Prominent species include *Poa scabrella*, *Aspidotis densa*, *Luzula campestris*, *Hieracium scouleri*, *Iris chrysophylla*, and *Thlaspi montanum* var. *montanum*; other important species are *Ranunculus occidentalis*, *Monardella villosa*, and *Silene hookeri*.

Within the successional pattern for lower elevation serpentine sites observed by White (1971), the vegetation at Beatty Creek appears to be between the intermediate and climax stages. *Ceanothus cuneatus* and *Aspidotis densa*, two species considered indicative of intermediate successional status, are present. However, the *Pinus jeffreyi* savanna is well-developed here, and perennial grasses and forbs are the major components of the herbaceous flora. Overall, the Beatty Creek community is a good example of a *Pinus jeffreyi*/grass savanna association.

Many of the other 21 populations of *P. capitata* occur in communities with habitat features and vegetation fairly similar to the one studied above. Notable exceptions are at Red Mountain and Goolaway Gap. These represent the highest elevations where *P. capitata* was studied (see Table 3), and the associated plant communities are different from the one described at Beatty Creek. No quantitative studies were conducted at these sites, but partial lists of associated species at each location are of interest. At the Red Mountain site, unique associates include *Pinus lambertiana*, *Garrya buxifolia*, *Amelanchier* *pallida*, and *Silene campanulata* ssp. *glandulosa*. At the Goolaway Gap site, associated species not noted at other locations include *Arctostaphylos viscida*, *Ceanothus pumilus*, *Castanopsis chrysophylla*, *Whipplea modesta*, and *Vicia californica*.

The Boomer Hill I and II sites appeared unique as well, occurring at higher elevations than Beatty Creek and in more mesic situations. Associated species at the Boomer Hill I site include *Phacelia hastata*, *Rubus ursinus*, *Lathyrus polyphyllus*, *Bromus rigidus*, *Hypericum perforatum*, *Cynosurus echinatus*, *Torilis arvensis*, *Polystichum munitum*, *Lonicera hispidula*, *Vicia sativa*, *Verbascum thapsus*, *Collomia heterophylla*, and *Montia perfoliata*. As noted previously, the soils at this site appear to be of a different, less stringent chemical nature than the more typical serpentine soils of other *P. capitata* sites.

The Boomer Hill II site includes *Salix* sp., *Aquilegia formosa*, *Petasites frigidus*, *Equisetum arvense*, *Veronica americana*, *Chrysanthemum leucanthemum*, and *Trifolium dubium*. This site is unusual in the high amount of seepage which occurs from the gentle slopes.

There were only two *Phacelia capitata* sites where *Pinus jeffreyi* was not noted: Boomer Hill I and Bridge. Otherwise, the species is associated with *P. jeffreyi* (in varying amounts) throughout its range.

Vegetation history

Due to a long, complex geologic history, dissected topography, edaphic diversity, and a steep climatic gradient from the coast inland, the Klamath Mountains have evolved to contain a very wide range of habitats. These factors have had a major influence on the vegetation types that have come to exist in the region. The most striking characteristics of Klamath vegetation are summarized by Whittaker (1961): 1) the area has one of the most highly complex vegetation patterns in North America; 2) forest formations thought to most closely resemble Arcto-Tertiary forests (redwood and mixed evergreen communities) occur there; and 3) the region has an exceedingly rich flora for its latitude, and is a center of floristic diversity and narrow endemism. The vegetation history giving rise to these characteristics must have been extremely complex. A summary is offered here, to aid in postulating about the evolutionary history of *Phacelia capitata*.

The vegetation history of the Pacific Northwest has been considered by Detling (1968); that of the Klamath region in particular was discussed by Whittaker (1961). According to the former, there have been three principal sources of plant associations in the Pacific Northwest: 1) evolution *in situ*; 2) the northern Arcto-Tertiary Geoflora; and 3) the Madro-Tertiary Geoflora of western Mexico and the southwestern United States. The movements of these Geofloras began during the Oligocene epoch, as a drying and cooling trend allowed the replacement of Eocene subtropical forests by more temperate forests of Sequoia and Metasequoia across much of the Pacific Northwest. These forests comprised the Arcto-Tertiary Geoflora, and their spread across the region continued into the Miocene epoch. During the late Miocene, continued cooling and increasingly dry conditions affected the Arcto-Tertiary forests, leading to a decrease in deciduous forms and restriction of these forests to the more humid coastal strip (Whittaker, 1961). A general increase in members of the Pinaceae and dry-adapted herbaceous types accompanied these changes (Detling, 1968). The spread of these latter dry-adapted vegetation types, many of which moved northward from probable centers of origin in scattered areas of the southwest, was very important to the flora of the Pacific Northwest; these assemblages comprised the Madro-Tertiary Geoflora. This flora reached southwestern Oregon by early in the Pliocene epoch, and reached its maximum development there by the middle of the epoch (Detling, 1968). It is thought that during the Pliocene epoch the vegetation of the Klamath Mountains took on essentially its present-day character (Whittaker, 1961).

During the late Pliocene, a further cooling trend culminated eventually in the ice ages of the Pleistocene epoch. At least four periods of glacial advance and retreat occurred, leaving northern relict species at higher elevations mixed with more xeric, southern vegetation types (i.e., the Pine-oak Forest) throughout the Pacific Northwest (Detling, 1968). More recently, a xerothermic period dryer and warmer than the present, the Hypsithermal interval, occurred 4-8,000 years ago. The northward spread of the Madro-Tertiary Geoflora resumed and continued. This trend brought new genera and species over the Klamath Mountains from northern California, and chaparral vegetation became established in the Rogue River basin (Detling, 1968).

The events of the last 4,000 years, under a cooler, moister climatic trend, are summarized by Detling (1968).

> With possible temporary unrecorded reversals the Mesic Coniferous Forest has again become dominant over much of the western portion of the region. It has largely replaced the xeric Rogue flora except for numerous refugia where soil conditions have probably hindered its (the xeric flora's) competitors.

Serpentine areas of southwestern Oregon are perhaps good examples of such soil-influenced refugia.

The end results of these historical events are presented by Whittaker (1961).

> The central relation of the Klamath Region is regarded primarily not as one of a center of origin for forests of other parts of the West, but as a center toward which mesophytic forests of the past have shrunk, and as a center of accumulation of species of varied evolutionary history in the diverse habitats of ancient land surfaces.

In summary, it is interesting to note that 28 genera, out of 53 considered by Detling (1968) to be important members of the Madro-Tertiary Geoflora, extend into the Pacific Northwest. Phacelia capitata is found in association with nine of these 28 genera: *Amelanchier*, *Arbutus*, *Arctostaphylos*, *Ceanothus*, *Garrya*, *Holodiscus*, *Pinus*, *Rhus*, and *Umbellularia*. In the genus *Pinus*, *P. jeffreyi* has as its area of northernmost distribution the geographic region to which *Phacelia capitata* is restricted. It seems reasonable to postulate that the *Pinus jeffreyi*/grass woodland, with which *Phacelia capitata* is frequently associated, may be a good example of one of the diverse communities of Madro-Tertiary derivation which entered the Klamath Region from the south.

BIOSYSTEMATIC STUDIES

Cytology

Materials and methods. For chromosome counts from microsporocytes, floral buds were obtained in the field by collecting several young inflorescences from the plants. These inflorescences were immediately placed in a killing and fixing solution of 3 parts 95% ethanol: 1 part glacial acetic acid, which was mixed in the field, for 24 hours. The material was then washed in two overnight changes of 70% ethanol, and stored in a freezer in a third change of the same.

In the buds of the helicoid cymes there is a distal progression of meiosis throughout the early growing season (late April-late May). The entire inflorescences were therefore stained, using the alcoholic hydrochloric acid-carmine stain described by Snow (1963), to ensure that suitable buds were obtained. Inflorescences were warmed in the stain for 24-48 hours in a 55-60°C oven, were then rinsed briefly in distilled water and studied immediately, or were stored in 70% ethanol in a freezer. Anthers were dissected from the buds and placed on a slide in a drop of 45% acetic acid. A cover slip was placed on the material and the cells were squashed by applying pressure. Often, several buds from one inflorescence had to be prepared before an appropriate meiotic stage was observed.

Results. Twenty-eight chromosome counts were made in the course of this study: 20 for *Phacelia capitata*, five for *P. corymbosa*, two for *P. heterophylla*, and one for *P. hastata*. These results, plus previous counts for *P. capitata* and *P. corymbosa*, are shown in Table 6.

The base chromosome number in the species group *Magellanicae* is x=11 (Heckard, 1960). At 19 of 20 sites counted, *P. capitata* occurs at this chromosome level. Of particular interest are two populations, Elk Creek and Callahan Creek, which contain tetraploid individuals. The Elk Creek population is a mixture of diploids and tetraploids. Further counts from the Callahan Creek site may reveal the presence of diploids there, as well. Thus, all six species in the *Magellanicae* that occur as basic diploids are now known to have morphological counterparts at the tetraploid level.

Two previous tetraploid counts (n=22) for *P. corymbosa* in Oregon were cited by Heckard (1960). These, plus five additional counts obtained during this study, indicate that *P. corymbosa* occurs primarily at this level in Oregon. Diploids of this species are known to occur in the North Coast Ranges of California, and in one locality in the Sierra Nevada (Heckard, 1960). Further counts may yet reveal the existence of diploids of *P. corymbosa* in Oregon.

Three counts for *P. heterophylla* in southwestern Oregon, all n=11, had previously been recorded (Heckard, 1960). The two additional counts reported here indicate that this species (as ssp. *virgata*) is primarily

Table 6. Chromosome numbers for _Phacelia_ species group _Magellanicae_ in southwestern Oregon.

Species	Population	Chromosome number (n)	Collection
P. capitata	Beatty Creek	11	Shelly 419
	Bilger Creek	11	Shelly & Nelson 724
	Boomer Hill I	11	Shelly & Holmes 766
	Boomer Hill II	11	Shelly & Holmes 781
	Bridge	11	Kruckeberg 2703
	Callahan Creek	22	Shelly 440
	Cow Creek I	11	Shelly 405
	Cow Creek II	11	Shelly 411
	Cow Creek Turn-off	11	Shelly 681
	Doe Creek	11	Shelly 706
	The Drew	11	Shelly & Nelson 734*
	Elk Creek	11	Shelly & Nelson 726
	Elk Creek	22	Heckard 2930; Shelly 433
	Goolaway Gap	11	Shelly & Nelson 738
	Lee Creek	11	Shelly 399
	Little River	11	Shelly 690*
	Myrtle Creek North	11	Shelly 414
	Peel	11	Shelly 354*
	Red Mountain	11	Shelly & Nelson 736
	Salt Creek	11	Shelly & Nelson 725*
	Weaver Road	11	Shelly 689
P. corymbosa	Eight Dollar Mtn I	22	Shelly 700
	Eight Dollar Mtn II	22	Shelly 702
	Grave Creek	22	Shelly 441
	Rough & Ready	22	Shelly 698
	Waldo	22	Shelly 697
	Wimer Road	22	Constance & Bacigalupi 3394
P. hastata	Boomer Hill I	22	Shelly & Holmes 767
P. heterophylla	Cow Creek	11	Shelly 714
	Elk Creek	11	Shelly & Nelson 728

*-Representative voucher from the same population, the actual count being obtained from a separate, unvouchered individual.

diploid in that area, although it does occur at the tetraploid level elsewhere in its range, mainly as ssp. *heterophylla* (Heckard, 1960).

The count reported here for *P. hastata* is apparently the first one from southwestern Oregon. Only tetraploids of this widespread species have been found (Heckard, 1960).

Morphology of the species

Taximetric studies. The morphological characteristics of *Phacelia capitata* were studied, to describe the degree of diploid variation within the species and the variation pattern in the populations containing tetraploids. For comparative purposes, studies of *P. corymbosa*, *P. hastata*, and *P. heterophylla* ssp. *virgata* were also made.

Methods. Living plants were used in the numerical studies, due to a paucity of representative herbarium material of *P. capitata* and because the features of the corolla are obscured in pressed specimens. It was hoped that greenhouse studies could be conducted to augment the field studies. However, survival of transplants (8/29) of *P. capitata* and *P. corymbosa* was poor, possibly due to overwatering. Of the survivors, only one plant (*P. capitata*) flowered. Seed germination of *P. capitata*, with no pre-treatment, was good (80%), but none of these plants flowered.

A total of 530 individuals from natural populations was studied. For *Phacelia capitata*, 420 plants from 20 populations were examined. Boomer Hill II and Red Mountain were omitted, due to the small number of individuals present at these sites. With the exception of the Elk Creek (33 plants) and Bridge (27 plants) populations, 20 plants at each location were measured. Corolla measurements were not taken for the Goolaway Gap population, because the plants were not flowering at the times the site was visited.

For comparison with P. capitata, 110 individuals were studied representing other species of the Magellanicae: 80 of P. corymbosa (4 populations), 20 of P. heterophylla ssp. virgata (1 population), and 10 of P. hastata (1 population). Site locations and characteristics for these populations are listed in Table 7.

From each individual studied, data for 10 morphological characteristics were collected: blade length (mm), leaf width (mm), width of corolla opening (mm), corolla length (mm), calyx length (mm), stem height (cm), number of leaf lobes, type of leaf lobing, number of floral branches below the terminal cymes, and glandulosity.

The five leaf and flower characteristics were measured with a Zeiss 10x handlens which contains a 10 mm scale. Stem height was measured with a ruler, from the base of the flowering stem to the tip of the terminal cymes.

Qualitative assessments of the type of leaf lobing and the degree of glandulosity were made in the following manner:

Table 7. Study populations of *Phacelia corymbosa*, *P. hastata*, and *P. heterophylla* in southwestern Oregon.

Site	Population number (CLUSTER)	T	R	Sec	Location	County	Elev. (m)	Aspect	Slope %
P. corymbosa									
Eight Dollar Mtn I	0030	38S	8W	19	Siskiyou NF rd 4201 at Illinois River	Josephine	390	SW	0-15
Eight Dollar Mtn II	0040	38S	8W	8	Siskiyou NF rd 4103, 5 km W of Selma	Josephine	450	S	10
Grave Creek	-	33S	4W	21	Grave Ck Rd, 3.5 km N of Slate Ck Rd	Jackson	850	SE	5
Rough & Ready	-	40S	8W	18	Rough & Ready Botanical Wayside, 8 km S of Cave Junction	Josephine	425	-	0
Waldo	0020	40S	8W	28	Co Rd 5560, 4.2 km E of O'Brien	Josephine	475	SW	0-5
Wimer Road	0010	41S	9W	4	Siskiyou NF rd 4402 (Wimer Rd), 6.5 km SW of O'Brien	Josephine	490	SE	0-20
P. hastata	H010	Same as *P. capitata* Boomer Hill I population (see Table 3)							
P. heterophylla									
Cow Creek	E010	30S	7W	35	N side of Cow Ck, 0.1 km W of Doe Ck Rd	Douglas	300	S	0-30
Elk Creek	-	30S	2W	34	St Hwy 227, 0.8 km E of Tiller	Douglas	350	S	10

Type of leaf lobing

0-leaves entire.
1-leaves pinnatifid (lobes with a broad base at the midvein).
2-leaves pinnately compound (lobes reaching the midvein, with entire leaflets distinguishable).

Glandulosity (when viewed with 40x Zeiss dissecting microscope)

0-eglandular.
1-a few scattered glandular trichomes among the longer tapering trichomes, mainly in and near the inflorescence.
2-densely and conspicuously glandular, especially on intermediate-length trichomes in and near the inflorescence, on the pedicels, and on calyces.

Results. The means and standard deviations for the ten morphological characteristics were calculated for each population, and these are given in Table 8.

The basic organization of the plants in the Magellanicae consists of a tap root, modified by varying degrees of branching, and a simple or branched caudex, of which each axis bears a rosette and gives rise to an annual flowering stem. The stem pattern fundamentally consists of an axis, usually foliate (or bracteate), with branches bearing one to several helicoid cymes (Heckard, 1960).

Leaves. The size and outline of leaves are characters of fundamental importance in the Magellanicae. Heckard (1960) emphasized the importance of the "climax leaf type" (the mature rosette leaves produced just before formation of the flowering stem) in making comparisons, due to the large amount of variability possible within a

Table 8. Means and standard deviations for ten morphological characteristics measured on living plants from 26 *Phacelia* populations. Left figure in each population is the mean, right figure is the standard deviation. N=20 except as noted.

Phacelia capitata

Characteristic	Beatty Creek		Bilger Creek		Boomer Hill I		Bridge (n=27)		Callahan Creek		Cow Creek I		Cow Creek II		Cow Creek Turn-off	
Blade length (mm)	36.9	7.0	46.2	6.2	45.2	9.2	37.7	7.0	57.9	11.4	37.7	9.7	56.3	14.1	36.5	9.0
Leaf width (mm)	3.4	0.6	4.1	0.8	4.1	0.8	4.7	0.9	5.4	1.1	3.5	0.6	4.5	1.0	3.4	0.8
Corolla opening (mm)	5.3	0.9	4.2	0.5	3.4	0.6	4.9	0.7	5.8	0.8	3.9	0.7	4.4	0.9	3.8	0.4
Corolla length (mm)	5.8	0.5	5.7	0.4	5.8	0.4	5.3	0.4	6.6	0.7	5.6	0.5	5.6	0.5	5.6	0.4
Calyx length (mm)	5.0	0.6	5.3	0.6	5.4	0.4	4,0	0.5	5.3	0.6	5.2	0.7	5.2	0.9	5.1	0.5
Stem height (cm)	29.6	6.5	35.1	11.8	25.6	5.4	28.6	6.2	42.4	10.5	29.9	5.8	30.7	8.0	34.7	7.1
No. of leaf lobes	0	0	0	0	0	0	0.04	0.2	0	0	0	0	0.1	0.3	0	0
Type of lobing[1]	0	0	0	0	0	0	0.04	0.19	0	0	0	0	0.1	0.3	0	0
No. of floral branches	0.4	0.8	2.0	1.6	2.2	2.1	0.9	1.0	2.7	2.0	1.4	1.4	1.6	1.1	1.1	1.1
Glandulosity[2]	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0	1.1	0.2	1.1	0.2

1-Type of lobing:
0-leaves entire
1-leaves pinnatifid
2-leaves pinnately compound

2-Glandulosity:
0-eglandular
1-a few scattered glandular trichomes among the longer tapering trichomes, mainly in and near the inflorescence
2-densely and conspicuously glandular, especially on intermediate-length trichomes in and near the inflorescence, on the pedicels, and on calyces

Table 8. Continued.

Characteristic	*Phacelia capitata* (continued) Doe Creek		Doe/ Thompson Ridge		The Drew		Elk Creek (n=33)		Goolaway Gap*		Lee Creek		Little River		Myrtle Creek North		Peel	
Blade length (mm)	44.9	10.6	50.2	9.3	47.4	12.4	60.7	15.0	33.4	9.9	40.4	7.9	40.6	8.7	48.0	12.3	38.2	10.4
Leaf width (mm)	3.8	0.7	4.4	0.8	4.2	0.9	6.8	2.1	3.3	0.8	3.7	0.6	3.9	0.7	4.5	1.3	4.0	1.0
Corolla opening (mm)	4.5	0.6	5.3	1.0	4.9	0.7	7.0	0.8	-	-	4.1	0.7	4.6	0.5	3.9	0.4	4.7	0.8
Corolla length (mm)	6.1	0.4	6.6	0.6	6.1	0.4	6.8	0.5	-	-	5.7	0.4	6.1	0.6	5.5	0.4	6.2	0.6
Calyx length (mm)	6.0	0.7	6.1	0.6	6.0	0.7	5.6	0.7	4.7	0.6	4.8	0.6	5.0	0.5	5.2	0.6	4.8	0.5
Stem height (cm)	33.8	9.6	34.2	6.2	32.2	8.4	39.5	9.3	18.4	5.8	26.3	5.3	31.2	6.1	38.2	11.4	32.1	5.0
No. of leaf lobes	0.5	1.1	0.1	0.5	0.1	0.5	0.2	0.8	0	0	0	0	0	0	0	0	0.2	0.9
Type of lobing	0.3	0.6	0.1	0.2	0.1	0.2	0.2	0.6	0	0	0	0	0	0	0	0	0.1	0.5
No. of floral branches	3.2	2.5	3.2	2.5	1.8	1.4	3.0	1.9	1.1	1.7	1.7	2.4	1.3	1.0	3.3	4.5	1.0	0.7
Glandulosity	0.9	0.3	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0	1.0	0

*-Data are pre-flowering.

Table 8. Continued.

Characteristic	Phacelia capitata (continued)						P. corymbosa								P. hastata		P. heterophylla ssp. virgata	
	Rice Creek		Salt Creek		Weaver Road		Eight Dollar Mtn. I		Eight Dollar Mtn. II		Waldo		Wimer Road		Boomer Hill I (n=10)		Cow Creek	
Blade length (mm)	35.5	8.7	47.8	7.4	44.1	14.2	37.8	6.3	36.1	5.8	29.8	5.6	36.2	12.0	58.8	10.2	59.6	11.4
Leaf width (mm)	3.5	0.6	3.9	0.8	4.1	1.1	10.0	2.1	8.9	1.2	7.9	1.7	10.0	2.7	9.8	2.2	12.0	2.8
Corolla opening (mm)	5.0	0.8	4.0	0.7	4.1	0.7	7.3	1.0	7.1	1.4	7.0	1.3	6.8	0.8	7.2	0.7	5.2	0.8
Corolla length (mm)	6.4	0.5	5.4	0.6	6.0	0.5	7.3	0.6	6.8	0.6	7.6	0.8	7.1	0.9	6.8	0.5	5.4	0.4
Calyx length (mm)	5.4	0.6	4.9	0.9	5.4	0.9	5.1	0.6	4.8	0.7	5.5	0.5	5.1	0.7	6.2	0.8	4.5	0.5
Stem height (cm)	26.8	6.0	33.5	8.5	29.3	6.2	18.1	3.4	14.3	4.2	9.9	2.5	17.7	8.9	32.5	7.9	50.9	12.0
No. of leaf lobes	0	0	0	0	0.2	0.6	1.1	1.6	3.0	1.7	1.6	1.4	1.7	2.1	0.3	1.0	4.1	1.7
Type of lobing	0	0	0	0	0.1	0.3	0.7	0.9	1.7	0.7	1.2	1.0	0.9	0.9	0.2	0.6	1.8	0.4
No. of floral branches	1.3	1.7	2.6	3.1	1.9	1.7	1.8	0.4	1.5	0.5	1.0	0.5	1.6	0.5	3.9	2.5	17.4	6.9
Glandulosity	1.0	0	1.0	0	1.0	0	2.0	0	2.0	0	2.0	0	2.0	0.2	1.0	0	2.0	0

single plant. It was found in *P. capitata* that even on living plants these climax leaves were frequently withered at anthesis. For this reason, measurements were made on living leaves from sterile rosettes, which appeared to be as representative as possible. It is believed that this method provides an adequate comparison of the distinctive leaves of *P. capitata* with those of related species.

The sterile rosette leaves of diploid *P. capitata* are generally entire, although in six populations lobed leaves were observed. In these six cases combined, the number of lobed leaves was only 12 out of 147 observed. On these 12 leaves, the number of lobes varied from one to four; in two populations (Peel, Doe Creek), pinnately compound sterile rosette leaves were observed. Thus, lobing of such leaves is of infrequent occurrence in diploid *P. capitata*.

It should be noted that in 13 of the 18 diploid populations of *P. capitata* studied, and in both populations containing tetraploids, it could be determined whether the climax leaves of fertile rosettes were lobed or not. These results are shown in Table 9. Percent of climax leaf lobing in the 13 diploid populations ranged from 0% (Bridge) to 85% (Boomer Hill I); in nine of these 13 populations, lobed climax leaves were 50% or less of the total. Thus, the climax leaves do show a greater degree of lobing compared to sterile rosette leaves. However, climax leaf lobing is sporadic in occurrence

Table 9. Climax leaf lobing in *Phacelia capitata*.

Population	Number of stems observed with lobed climax leaves	%
Beatty Creek	6/20	30
Bilger Creek	4/20	20
Boomer Hill I	14/17	82
Bridge	0/27	0
Callahan Creek	13/20	65
Cow Creek II	7/20	35
Cow Creek Turn-off	2/20	10
Doe Creek	14/20	70
Doe/Thompson Ridge	6/16	38
The Drew	7/20	35
Elk Creek	18/33	55
Goolaway Gap	13/20	65
Rice Creek	10/20	50
Salt Creek	7/20	35
Weaver Road	11/20	55

and, since these leaves are frequently withered at anthesis, is of limited use in comparative studies.

The degree of leaf lobing is greater in both *P. corymbosa* and *P. heterophylla* than in *P. capitata*. In P. *corymbosa* the number of leaf lobes ranged from zero to six, but with entire leaves being infrequent. The nature of lobing ranges from pinnatifid to pinnately compound, sometimes within a single leaf (Heckard, 1960). In *P. heterophylla*, the number of leaf lobes ranged from one to eight; of the 20 individuals observed, 16 had pinnately compound leaves.

Heckard (1960) describes the leaves of *P. hastata* as being entire or occasionally with one to two pairs of lobes. The tendency for this species to possess entire leaves may have led to some of the early confusion of *P. leucophylla* (=*P. hastata*) with *P. capitata*. The leaves of *P. hastata* are usually longer and wider than those of *P. capitata*.

Leaf width was measured at the widest point of each blade; in lobed leaves, the widest point on the large, terminal lobe was measured. The narrow width of leaves in diploid *P. capitata* is distinctive. This characteristic, and the predominantly simple blades of sterile rosettes, are major distinguishing features of *P. capitata*.

Blade length (as measured from the base of the lowermost lobes in lobed leaves, and from the junction of the blade with the petiole in entire leaves) appears quite variable in diploid _P. capitata_. It is taxonomically useful to some extent, but not to the same degree as leaf outline and width.

Flowers. Throughout the _Magellanicae_, the flowers are biserial and crowded along the upper side of a circinate peduncle, forming a helicoid cyme (Heckard, 1960).

Corolla shape is significant for species comparisons in the _Magellanicae_. The extremes in shape are of two distinct types: a broad, open-campanulate corolla (i.e., _P. egena_); and a narrowly cylindrical corolla with the margins of the lobes incurved and embracing the stamens (i.e., _P. imbricata_). Between these extremes, the corolla types, though not sharply defined, are stable enough to delimit certain taxa (Heckard, 1960).

In this study, the width of the corolla opening (measured across the face of expanded flowers) and the length of the corolla (measured from the base to the tip of a lobe) were used to quantify corolla shape. In diploid _P. capitata_, the corollas are mostly cylindric, the lobes being neither spreading-campanulate nor incurved. Rarely, a few individuals showed some degree of spreading in the lobes (Boomer Hill I, Doe Creek, Doe/ Thompson Ridge).

The size of the corolla opening appears to be correlated with ploidy level. The Elk Creek and Callahan Creek populations of _P. capitata_, containing tetraploids, have the largest average corolla openings, exceeding the highest mean values for diploid populations. The corolla openings of P. corymbosa and P. hastata also are larger, on the average, than those of diploid P. capitata. The populations of the former two species are all tetraploid. The corolla openings of diploid P. heterophylla are within the range of diploid P. capitata, however.

Differences in corolla length show the same trends as width of the corolla opening. Again, there is a tendency for the tetraploid populations to have longer corollas than diploids.

The increased corolla size of tetraploids may be a result of the "gigas" effect (Stebbins, 1971), in which individuals of higher ploidy levels show a tendency for increased cell and organ size. Because of such apparent effects, corolla shape should be considered carefully when comparing these species.

The calyx length was also measured in flowers which were at full anthesis. The range of variation among all the species and populations overlapped considerably; this characteristic is thus probably of little use taxonomically.

Stem height. In considering height of stems in the Magellanicae, Heckard (1960) noted that, while such species as P. corymbosa (1-3 dm) and P. nemoralis (10-15 dm) show striking differences, the ranges of most species overlap considerably, "...limiting the utility of height as a taxonomic criterion." He also noted that, "...in general, there was no significant difference in height between diploid and tetraploid forms of the same species."

The results of this study indicate that there is a consistent difference in mean stem height between diploid _P. capitata_ (25.6-38.2 cm) and tetraploid _P. corymbosa_ (9.9-18.1 cm). The tall nature of the biennial _P. heterophylla_ is also distinctive. In the few _P. hastata_ plants studied, stem heights are similar to those encountered in diploid _P. capitata_.

There is a tendency for _P. capitata_ plants from the populations containing tetraploids to be larger than those from diploid populations, but individual observations from these two groups do overlap.

Floral branching. Heckard (1960) stated that the majority of inflorescence patterns within the _Magellanicae_ could be considered paniculate. Notable exceptions include those species having virgate inflorescences (i.e., _P. heterophylla_ ssp. _virgata_), in which numerous short floral branches overlap to form a densely branched system. The term "capitate" is defined by Heckard as "...the condition in which several congested cymes are more or less separate from other cymes and form a head."

In his description of _P. capitata_, Kruckeberg (1956) states that the inflorescence consists of two to three scorpioid cymes in a congested, subcapitate erect cluster that is usually borne singly and terminally. In this study, the number of floral branches below the terminal cymes was counted, to assess the variability of this feature. The results (Table 10) indicate that such branching is frequent in _P_. _capitata_ and is highly variable within and between populations. Even if one allows the presence of a single cyme below the terminal inflorescence to fit the "capitate" terminology used by Kruckeberg, it is still apparent that many of the flowering stems observed in _P_. _capitata_ show branching below the terminal capitulum. Exceptional individuals from diploid populations included plants with 13 and 17 (Myrtle Creek North), 14 (Salt Creek), 10 (Lee Creek), and 9 (Boomer Hill I and Doe/Thompson Ridge) cyme branches below the terminal cluster.

Of the 80 stems of _P_. _corymbosa_ studied, all had zero, one, or two cymes below the terminal cluster; 38 stems had two such cymes. Thus, for the tetraploid populations studied in Oregon, this species is not branched to the same extent as diploid _P_. _capitata_. The virgate inflorescence of _P_. _heterophylla_ ssp. _virgata_ is distinctive. Further studies of _P_. _hastata_ would be necessary to fully assess cyme branching in that species.

It is interesting to speculate on the extent to which the variable, sometimes high, degree of inflorescence branching in _P_. _capitata_ may be a phenotypic response to habitat disturbance. Of the three populations studied whose habitats are largely undisturbed (Rice Creek, Beatty

Table 10. Floral branching below the terminal cymes in *Phacelia capitata*.

Population	Occurrence of floral branches below the terminal cymes		Occurrence of more than one floral branch below the terminal cymes	
	Number	%	Number	%
Beatty Creek	6/20	30	1/20	5
Bilger Creek	17/20	85	12/20	60
Boomer Hill I	16/20	80	14/20	70
Bridge	15/27	56	6/27	22
Callahan Creek	19/20	95	12/20	60
Cow Creek I	15/20	75	7/20	35
Cow Creek II	17/20	85	10/20	50
Cow Creek Turn-off	12/20	60	7/20	35
Doe Creek	18/20	90	14/20	70
Doe/Thompson Ridge	20/20	100	14/20	70
The Drew	16/20	80	10/20	50
Elk Creek	32/33	97	28/33	85
Goolaway Gap*	11/20	55	4/20	20
Lee Creek	16/20	80	5/20	25
Little River	15/20	75	9/20	45
Myrtle Creek North	17/20	85	9/20	45
Peel	15/20	75	5/20	25
Salt Creek	19/20	95	11/20	55
Rice Creek	12/20	60	5/20	25
Weaver Road	15/20	75	11/20	55

*-Data from pre-flowering individuals.

Creek, and Bridge), the latter two contained the smallest proportions of individuals with two or more cyme branches below the terminal ones. The majority of other stems of diploid P. capitata came from highly disturbed areas, such as exposed roadbanks and rock pits. Further studies would be needed to determine the nature of this possible relationship and to define what factors, e.g., improved soil texture, might be influencing it.

Vestiture and glandulosity. Heckard (1960) described the two basic types of trichomes in the Magellanicae, the common tapering trichome and the glandular trichome. The tapering trichome may be erect or appressed. It exhibits a wide range of sizes, the extremes of which may give the appearance of two distinct types of tapering trichomes: large trichomes reaching lengths of four to five mm, and smaller trichomes which often form a velutinous undersurface beneath the large ones.

The septate glandular trichomes, when present, are part of the velutinous covering of shorter trichomes. They are most prevalent on upper parts of the stem, calyx lobes, pedicels, peduncles, petioles, and the veins of leaves. The glandular trichomes are often obscured because of their small size and relative infrequency among the small, tapering trichomes. They are readily observable on the upper portions of the stem, etc., using a 40x dissecting microscope.

Kruckeberg (1956) stressed the eglandulosity of P.

capitata. The results of my study indicate, however, that the species does possess short, glandular trichomes throughout its populations. Only one individual (Doe Creek) possessed no discernible glandular trichomes; two individuals (Cow Creek II, Cow Creek Turn-off) appeared conspicuously glandular. It is important to emphasize that the glandular trichomes of P. capitata are only visible microscopically. They are most abundant on the stem near the inflorescence, on the pedicels, and on the calyx lobes; they are less frequent on the leaves.

Phacelia corymbosa is readily distinguishable from P. capitata by its conspicuous dense glandulosity, in which the short- to medium-length trichomes are all gland-tipped (see SEM section). Phacelia hastata shows patterns of glandulosity similar to P. capitata. Phacelia heterophylla was seen to be quite glandular, and resembled P. corymbosa in this respect, at least on the stems in the inflorescences.

The leaf vestiture of P. capitata is illustrated in the SEM section.

Species description. A revised description of Phacelia capitata, modified from that of Kruckeberg (1956), is presented. Plants are deeply taprooted cespitose perennials with 1-many thin, wiry flowering stems each arising from a rosulate tuft of leaves, with numerous sterile leaf rosettes often present; stems are erect, unbranched or occasionally branched, (11)20-45(63) cm tall, finely sericeous, the silvery-gray herbage consisting of a hyaline-shiny pubescence made up of three trichome types: longer, appressed bristles underlain by shorter, matted trichomes, and with scattered, very short glandular trichomes, especially near the inflorescence, on the pedicels, calyx lobes, and leaf veins, rare or absent on the lower portion of the stem; sterile leaves of the basal rosettes are linear-lanceolate, simple and entire, very rarely pinnatifid or pinnately compound with 1-2 pairs of basal lobes, (1.7)2.5-6.5(8.8) cm long, (2.3)2.9-6.0(13.0) mm wide, tapering to petioles 1-2 cm long; climax leaves are entire, or occasionally have 1-2 basal lobe pairs; cauline leaves are gradually but not wholly reduced upwards; inflorescences consist of 2-3 helicoid cymes in a congested, capitate or subcapitate cluster borne singly or terminally, or frequently with 2 or more lateral cyme branches below the terminal cymes; pedicels in early fruit are 1-3 mm long, hispid; calyx lobes are linear-oblong, (3.0)4.2-6.6(7.7) mm long, 0.5-0.8 mm wide, with long-hispid margins, the abaxial surface short-hirsute; corollas are white, rotate, cylindric, or occasionally slightly campanulate-spreading, (4.1)5.0-6.9(8.0) mm long, (2.3)3.0-6.0(8.4) mm broad, with entire, obtuse-rounded lobes; appendages are attached barely a millimeter above the base of the corolla tube, the free portions forming a long (3 mm) and narrow "V" distally; stamens and style are exserted 5-7 mm, the filaments glabrous or with a few scattered hairs about mid-length along the filament; immature capsules are ovoid, 2-3 mm long, densely clothed with stout bristles 2 mm long; mature seeds are 1.9-3.0 mm long (in diploid specimens), brown, with a reticulate-pitted surface; n=11, 22.

Cluster analysis. To summarize the results of the taximetric studies, the mean values for the 10 morphological attributes measured for 25 study populations were subjected to cluster analysis using the computer program CLUSTER. The Goolaway Gap population of Phacelia capitata was omitted from the analysis because data for this site were collected prior to flowering.

Methods. The program CLUSTER is hierarchical, agglomerative, and combinatorial in nature; thus, dendrograms summarizing the clustering process are obtainable (Keniston, 1978). CLUSTER is interactive, as well; many possibilities exist for transformation or standardization of the data set, and for selection of different fusion strategies and dissimilarity measures. This introduces subjectivity into the process of data analysis, i.e., one must actually choose between various options until the most satisfactory results are obtained. Nonetheless, CLUSTER allows for a useful summary of the degrees of difference between the species and populations studied.

In this analysis, the Bray-Curtis dissimilarity index has been utilized. A feature of this index is that attributes with high scores largely determine the value of the measure, whereas attributes with low scores are relatively unimportant (Boesch, 1977). Thus, in this instance, values for leaf length and stem height would largely determine the cluster results. Due to this, and because four attributes (type of leaf lobing, number of leaf lobes, number of cyme branches below the terminal cluster, and glandulosity) were assessed in a qualitative or non-metric way, the data require standardization (Dr. C. D. McIntire, pers. comm.). The standardization method used was division by the attribute maximum, in which all values for a given morphological attribute are divided by the maximum value observed for that attribute. This removes the "high score bias," and allows use of quantitative and qualitative values together.

The fusion strategy defines the way in which group/ individual and group/group resemblances are calculated, and thus defines the final clusters which are formed. In the group average strategy, inter-group resemblance is defined as the mean of all resemblances between members of one group to members of another. Thus, group average clustering has no tendency toward "space distortion." As a result, it produces only moderately sharp clustering, but introduces relatively little distortion to the relationships originally expressed by the dissimilarity measure (Boesch, 1977). The group average fusion strategy best summarizes the differences which exist between the Phacelia species and populations studied.

Results. The results of the cluster analysis are shown in Figure 3. The four major clusters of interest are seen at a dissimilarity level of approximately 0.12. They include, from left to right, 1) diploid P. capitata (17 populations), 2) two P. capitata populations containing tetraploids and P. hastata (one population), 3) P. corymbosa (four populations), and 4) P. heterophylla ssp. virgata (one population).

The results indicate that, at least on the basis of mean values, the diploid populations of P. capitata are fairly uniform morphologically. The actual degree of variation within the species, especially with respect to leaf size and outline, and floral branching, were discussed above.

The similarity expressed between the populations containing tetraploid P. capitata and the P. hastata population is of interest, but it does not "prove" that these are the intergrading taxa at the former sites (Elk Creek and Callahan Creek). The similar tendencies toward longer, entire leaves, larger corolla openings and lengths, and intermediate glandulosity have most likely contributed to these three populations being clustered together. The actual source of morphological variation in the P. capitata populations containing tetraploids, which is problematic, is considered in the final section.

Figure 3. Cluster analysis of *Phacelia* species. (*Phacelia capitata*=A: 010-Little River; 020-Peel; 030-Lee Creek; 050-Bilger Creek; 060-Myrtle Creek North; 06A-Weaver Road; 070-Rice Creek; 080-Boomer Hill I; 090-Beatty Creek; 120-Cow Creek I; 130-Cow Creek II; 140-Salt Creek; 150-Doe/Thompson Ridge; 15A-Doe Creek; 160-Cow Creek Turn-off; 170-Elk Creek; 180-Callahan Creek; 190-The Drew; 210-Bridge; *P. corymbosa*=O: 010-Wimer Road; 020-Waldo; 030-Eight Dollar Mtn. I; 040-Eight Dollar Mtn. II; *P. hastata*=H: 010-same site as Boomer Hill I above; *P. heterophylla* ssp. *virgata*=E: 010-Cow Creek. See Tables 3 and 7 for population locations.).

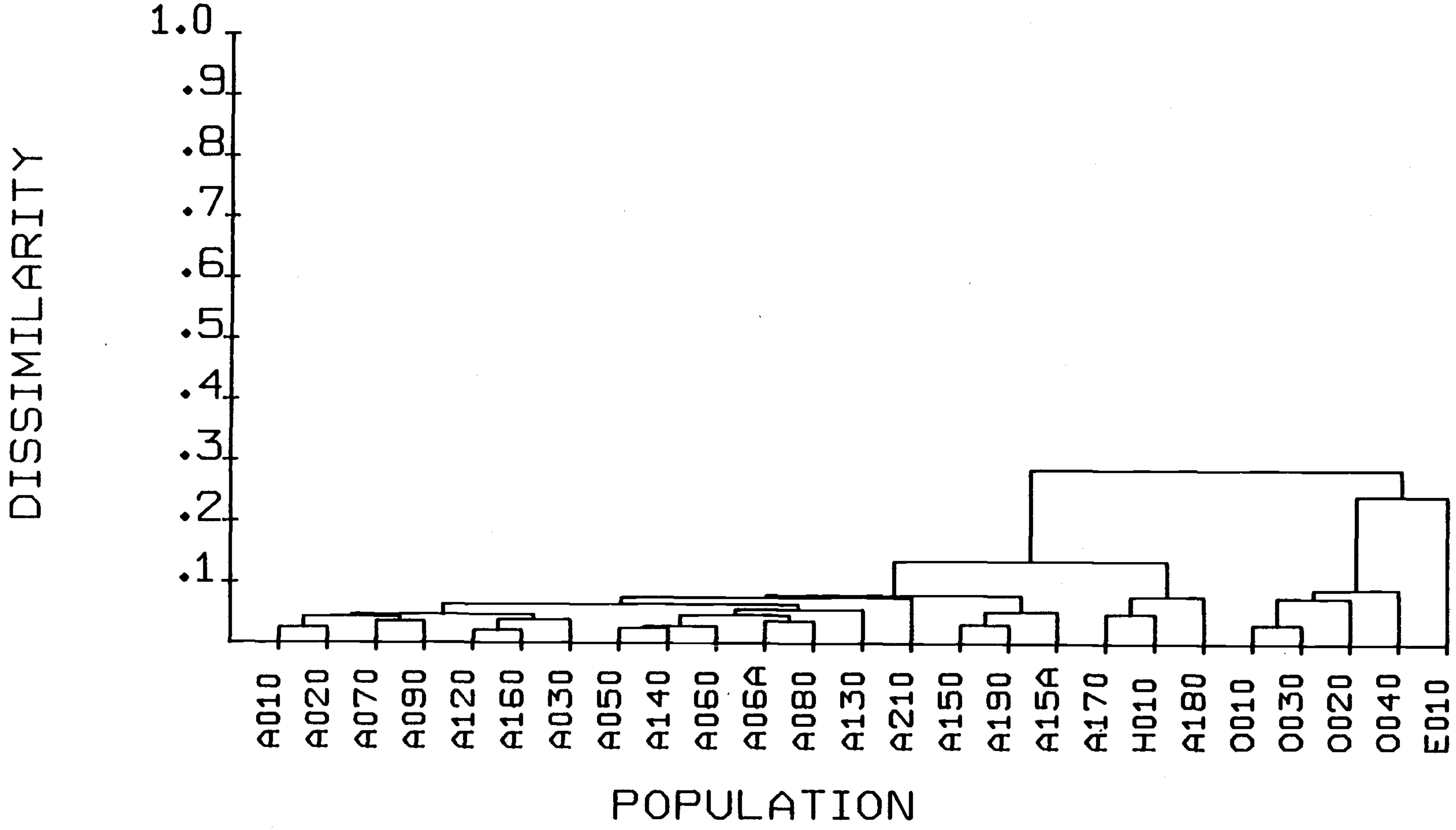


Figure 3. CLUSTER ANALYSIS OF PHACELIA SPECIES
ATTRIBUTE MAXIMUM STANDARDIZATION
BRAY-CURTIS DISSIMILARITY INDEX
GROUP AVERAGE FUSION STRATEGY

Cluster analysis appears to be useful in illustrating the major differences which exist in the species group Magellanicae, at least when well-defined entities (i.e., P. corymbosa, P. heterophylla ssp. virgata, and diploid P. capitata) are compared.

The major morphological differences between Phacelia capitata, P. corymbosa, P. hastata, and P. heterophylla ssp. virgata are summarized in Table 11.

Scanning electron microscopy. Methods. Seeds of Phacelia capitata and P. corymbosa, pollen morphology and leaf vestiture of P. capitata, and upper stem vestiture of P. capitata and P. corymbosa were studied using scanning electron microphotographs. The seeds used were dry, mature specimens. All pollen, stem segments, and leaves were taken from herbarium specimens and hydrated; they were then critical-point dried following the procedure of Cohen, et al. (1968). All specimens were then mounted on aluminum studs using Duco adhesive (Microstick adhesive for pollen), coated with approximately 180 angstroms of 60-40 gold-paladium alloy in a vacuum evaporator, examined, and photographed. The photography was done by the Oregon State University Scanning Electron Micrography Lab, Department of Botany and Plant Pathology.

Results. The reticulately ridged and pitted seed coat is similar in P. capitata (Figure 4A) and P. corymbosa (Figure 5A); this feature is shared by all species of the Magellanicae (Heckard, 1960). Of particular interest is

Table 11. Comparison of *Phacelia capitata*, *P. corymbosa*, *P. hastata*, and *P. heterophylla* ssp. *virgata* in southwestern Oregon.

Species	n	Habit	Stem height (cm)	Leaf outline	Leaf size		Inflorescence	Corolla shape	Glandulosity
					length(cm)	width(mm)			
capitata	11,22	perennial, mat-forming	20-45	linear-lanceolate, entire; rarely, with 1-2 pairs of leaflets at base of lamina	2.5-6.5	2.9-6.0	Cymes often terminal, or sub-terminal,or with 1-many lateral inflorescences below the terminal cymes	cylindric (campanulate in tetraploids)	scattered, very short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins
corymbosa	22	perennial, mat-forming	7.5-25	linear to lance-oblong, entire, or often with 1-2 pairs of leaflets at base of lamina	2.4-5.2	6.0-14.0	cymes terminal, or often with 1-2 sub-terminal cyme branches	cylindric-campanulate	conspicuosly glandular overall, with short-medium glandular trichomes
hastata	22	perennial, with 1-many stems, rarely mat-forming	20-50	lanceolate, entire, or rarely with 1-3 leaflets	3.5-7.5	7.0-13.0	cymes terminal or sub-terminal, often with 1-many lateral inflorescences below the terminal cymes	cylindric-campanulate	scattered, short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins
heterophylla ssp. *virgata*	11	biennial	30-75	pinnately dissected, with 1-4 pairs of lobes	3.8-8.0	8.0-17.0	virgate, with 10-many overlapping lateral cymes	cylindric-slightly flaring	medium-length glandular trichomes frequent in the upper portions of the inflorescence

Figure 4. Seed of _Phacelia_ _capitata_.

A Dorsal surface (50X)

B Portion of dorsal surface (150X)

C Dorsal surface pit detail (340X)

D Detail of a double "pore" complex (700X)

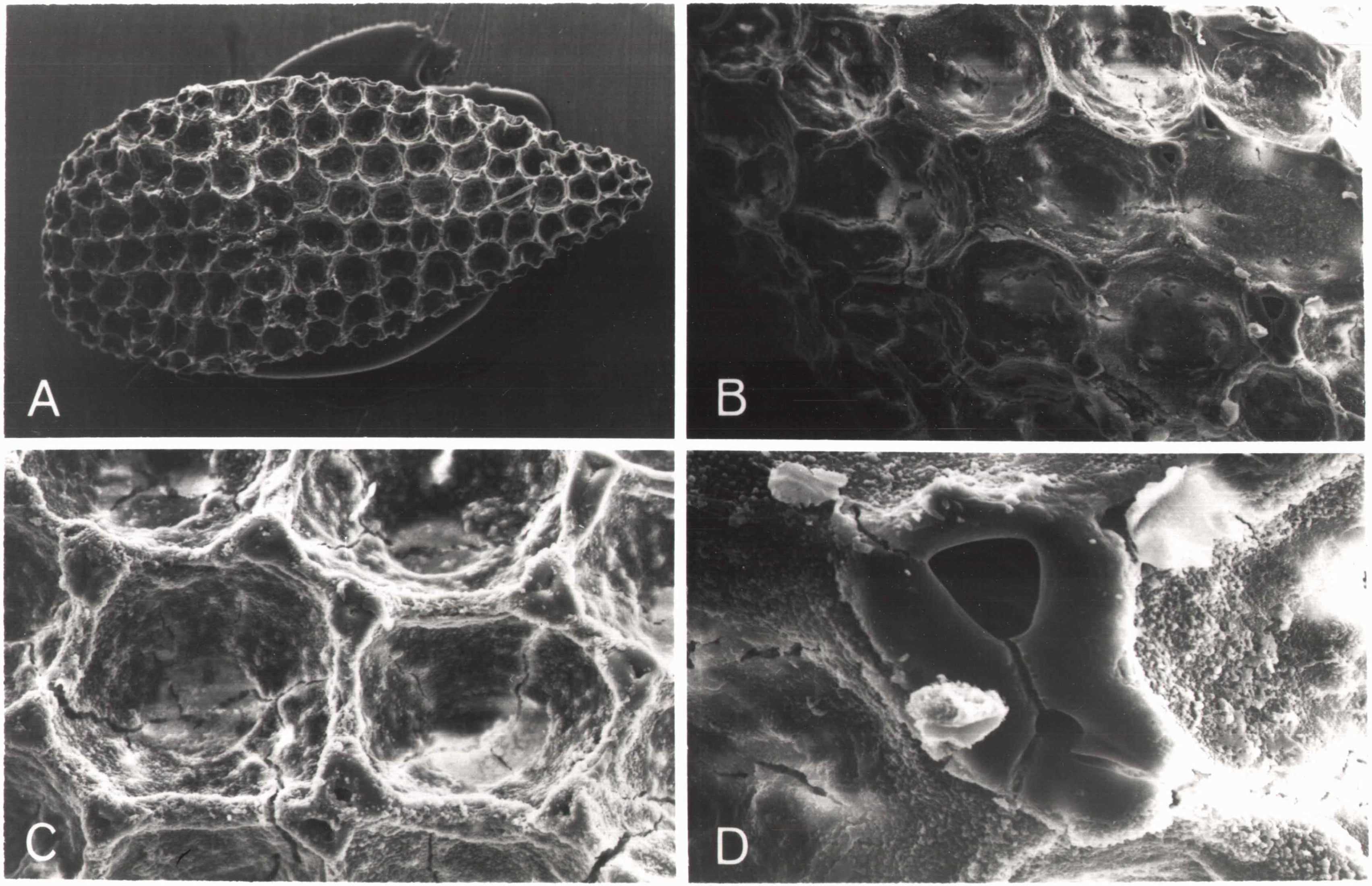


Figure 4.

Figure 5. Seed of <u>Phacelia corymbosa</u>.

A Dorsal surface (40X)

B Portion of dorsal surface (160X)

C Dorsal surface pit detail (280X)

D Detail of "pore" (1600X)

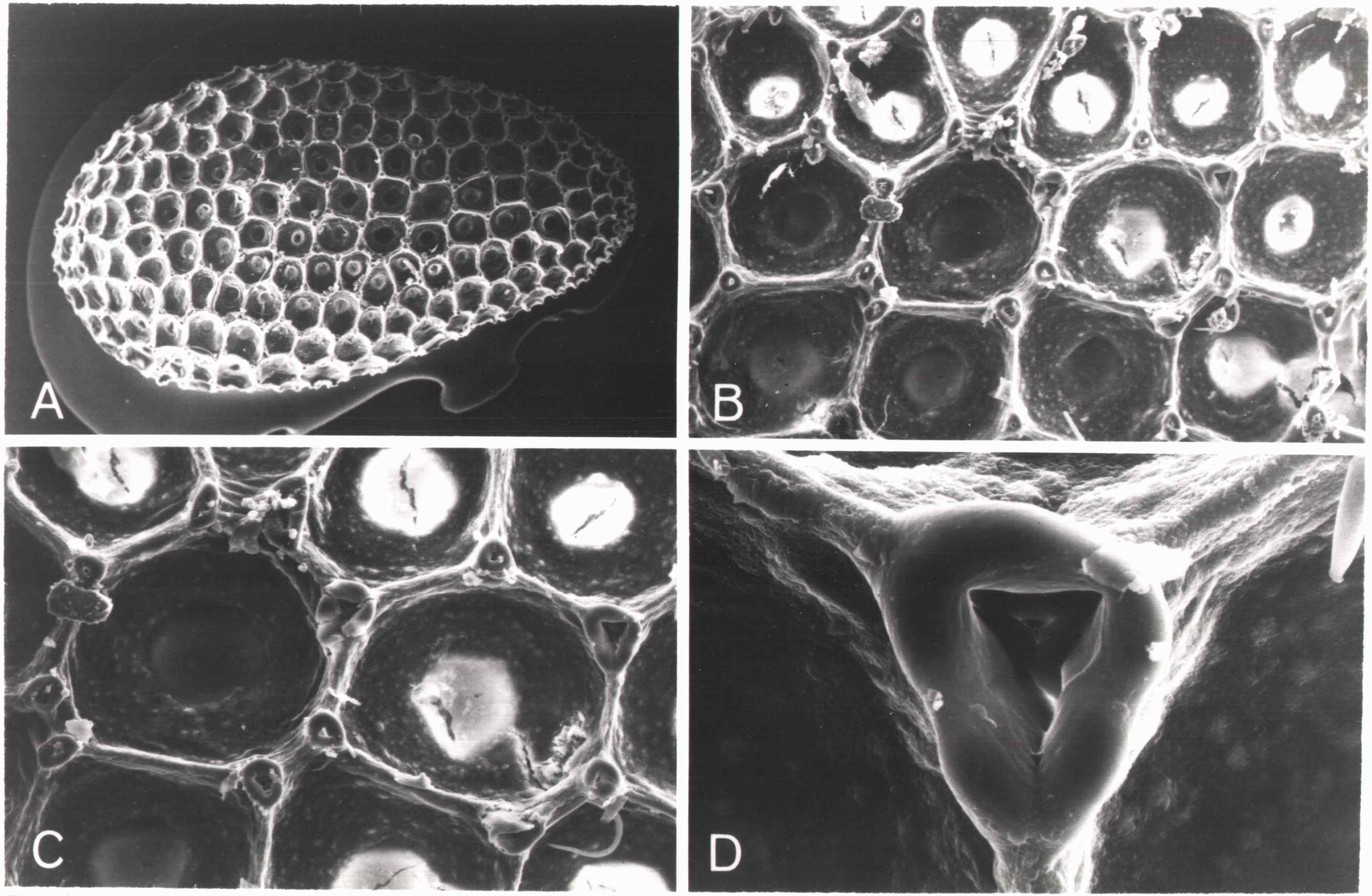


Figure 5.

the presence, in both species, of a set of distinctively distributed structures ("pores") associated with the junctions of the pit margins (Figures 4B-D, 5B-D). These "pores" appear to be bordered by hardened cell-wall material, and they may provide seemingly open (Figure 4D) or more constricted (Figure 5D) channels through the seed coat. The presence of such seed "pores" in other species of the Magellanicae, or in the genus Phacelia, has apparently not been previously documented. Intriguing possibilities for study concerning the function of these "pores" include supplying of oxygen to the embryos, regulation of seed dormancy (i.e., in P. corymbosa, which shows improved seed germination after cold stratification (Quick, 1947)), and/or facilitation of water imbibition.

Another peculiarity of seed coat morphology is prominent in P. corymbosa. In the bottom of each pit is a circular area of thin-looking material (Figures 5C, D). This "membrane" is frequently cracked, and when one layer is gone, a deeper lining is revealed in the pit bottoms; this second surface often has a small crack near its center. This "cracking membrane" system may also provide an interesting study in determining its possible relationship to seed germination ecology. These membranes do not appear to be as clearly developed in P. capitata (Figures 4B, C), seeds of which germinated well in the greenhouse with no cold stratification treatment.

An SEM study of pollen morphology in the

Hydrophyllaceae, by Constance and Chuang (1982), included two species in the *Magellanicae*, *P. heterophylla* and *P. imbricata*. The pollen grains of these species are described as tricolpate-tripseudocolpate, the colpi conspicuously baculate; the exine is finely and almost uniformly foveo-reticulate; the grains are isopolar, the colpi extending equally toward but not reaching either pole, the pseudocolpi nearly as long as the true colpi. The pollen of *P. capitata* fits this description closely (Figure 6A, B).

A surface view of the leaf vestiture in *P. capitata* illustrates the presence of the long, tapering trichomes, and the shorter trichomes which form a velutinous undersurface (Figure 6C). Magnification reveals the presence of small glandular hairs, in this case near the leaf margin, in the species (Figure 6D).

The conspicuous, medium-length glandular trichomes of *P. corymbosa* (Figure 7C) are very important in distinguishing it from *P. capitata* (Figure 7A). However, *P. capitata* is not eglandular (Figure 7B), since it does possess very small glandular trichomes similar to those which are found in *P. corymbosa* (Figure 7D).

Reproductive biology

Flowering and pollination biology. Flowering in *Phacelia capitata* begins in early May at the lower-elevation sites and continues until early to mid-June. At

Figure 6. Pollen and leaf vestiture of *Phacelia capitata*.

A Pollen grain (4500X)

B Detail of pollen grain colpus (18000X)

C Leaf vestiture (30X)

D Detail of vestiture at leaf margin (300X)

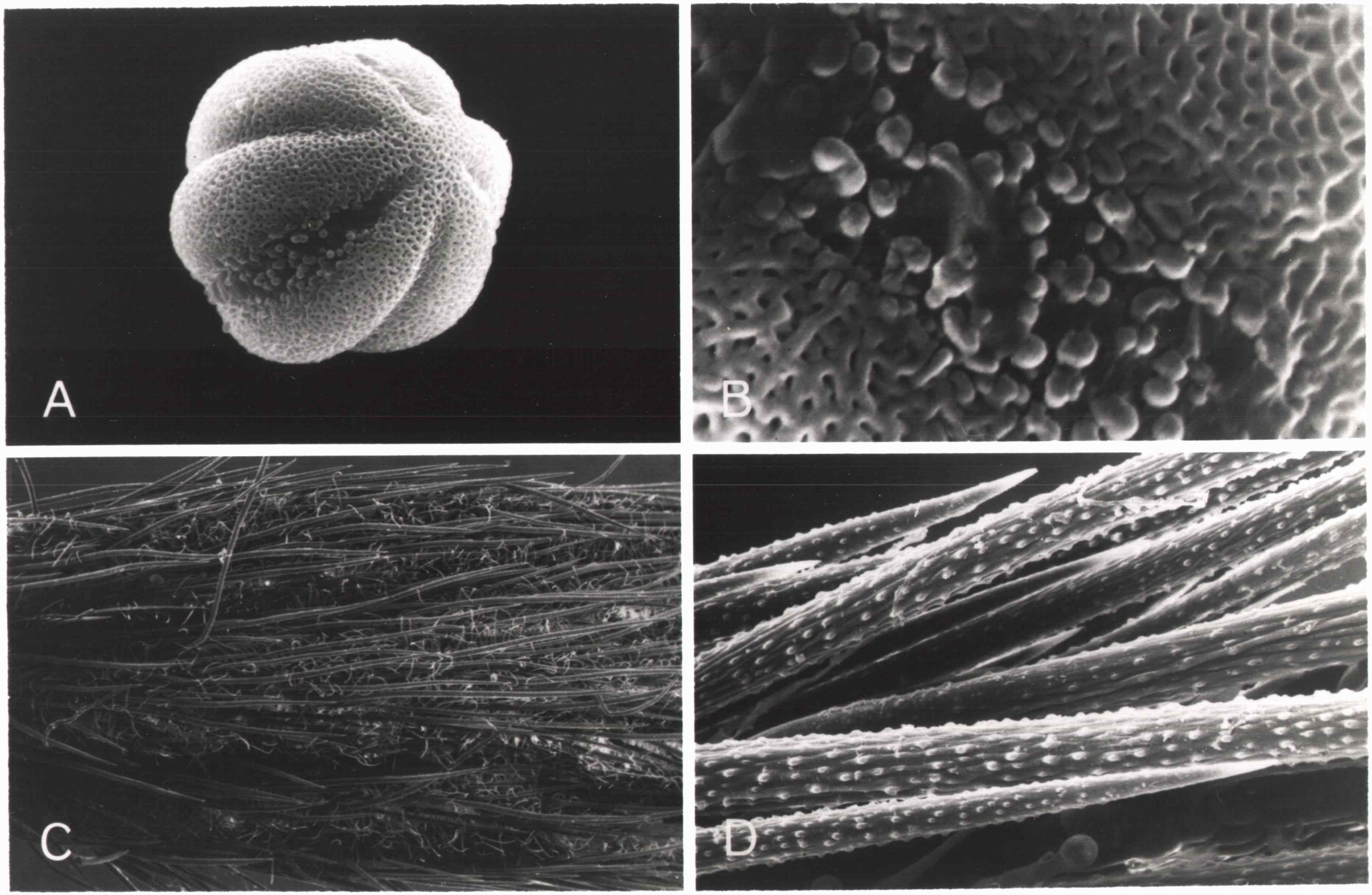


Figure 6.

Figure 7. Stem vestiture of *Phacelia capitata* and *P. corymbosa*; stem segments taken from just below the terminal cyme branches.

A *Phacelia capitata* stem vestiture (150X)

B Short glandular trichome of *P. capitata* (600X)

C *Phacelia corymbosa* stem vestiture (40X)

D Short glandular trichome of *P. corymbosa* (500X)

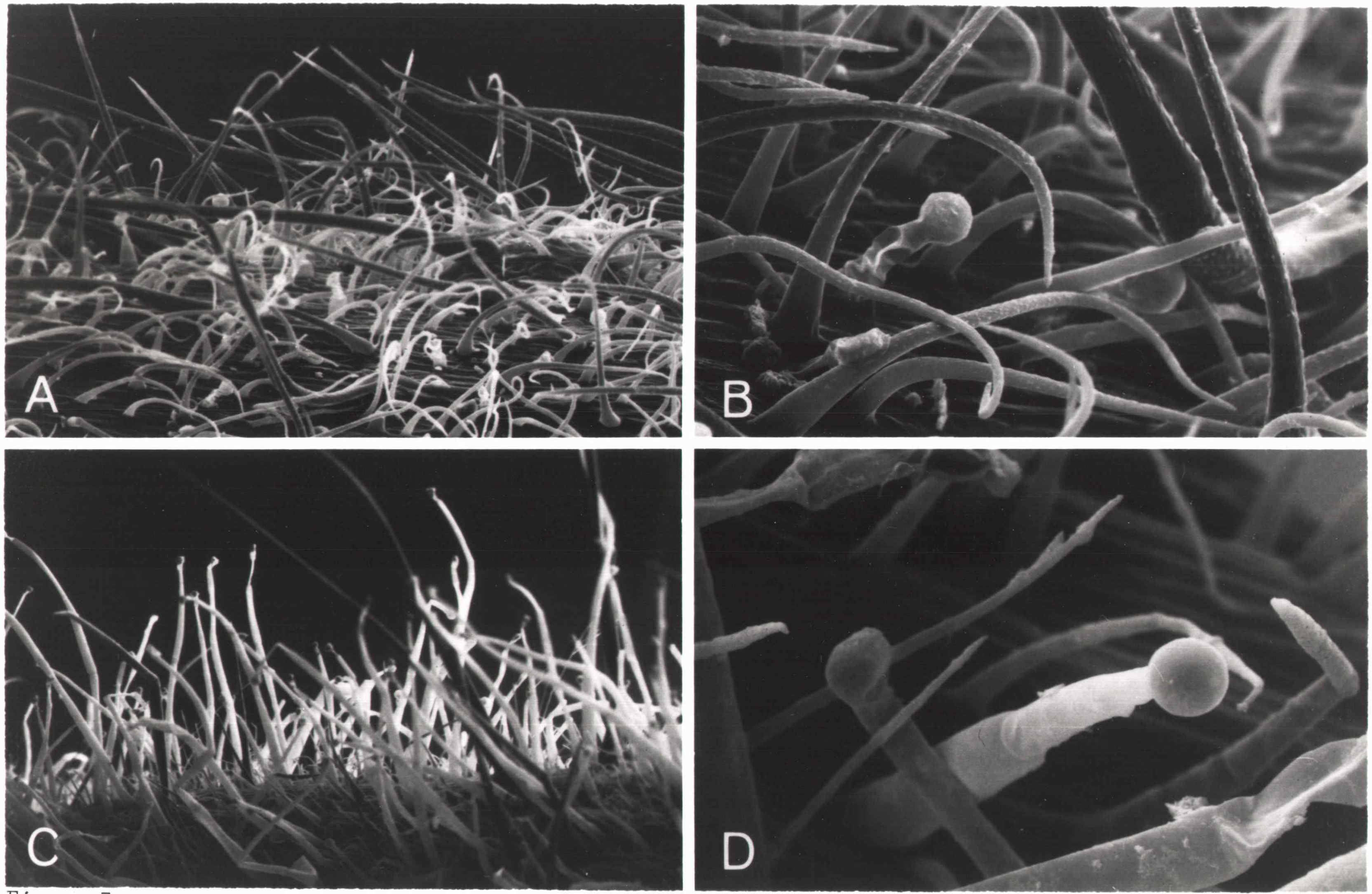


Figure 7.

the higher-elevation sites, initial flowering is delayed until late May or early June and lasts until early July. The first flowers to open within an inflorescence are on the lower portions of the cyme branches, although it was noted that the lowermost buds are not always the first to bloom. As flowering proceeds, the initially helicoid cyme branches uncoil until, at the time of seed maturation, they are nearly or completely ascending.

In flowers of _P_. _capitata_ which are fully expanded, the stamens and styles are well exserted, extending from 5-7 mm beyond the corolla tube. The anthers are subequal with the ends of the style branches. The stigmatic surfaces are very small, the stigmas being confined to the tips of the style branches and consisting of the ends of only a few cells (Heckard, 1960).

The flowers of _P_. _capitata_ are congested, forming a tight, many-flowered inflorescence which, as a whole, may be quite attractive to pollinators. In cases where the flowers in an inflorescence were counted, the number ranges from 53-303; these inflorescences varied from approximately 2.5 to 5.0 cm in diameter.

Throughout the _Magellanicae_, the flowers are protandrous, the pollen being ripe and available before the stigma is receptive (Heckard, 1960). This is one mechanism of dichogamy, or temporal separation of sex functions in flowers, whereby self-pollination may be inhibited. Protandry is only effective, however, if it is total, i.e., if all of the pollen is removed from a flower before the stigma is receptive (Faegri and van der Pijl, 1971). Another factor which may decrease the effectiveness of protandry as an inhibitor of self-pollination is the situation seen in the Magellanicae, in which flowering is protracted and many adjacent flowers of slightly differing ages may be open at one time on a single individual. The likelihood of having ripe pollen and receptive stigmas simultaneously within one inflorescence (as opposed to within single flowers) is undoubtedly increased in such a system. The congested arrangement of the flowers may make pollen transfer to such receptive stigmas likely.

Owing to the above factors, for self-pollination to occur in P. capitata, pollen must apparently be transferred from the anthers of one flower to the stigma of another flower on that same individual. This process is referred to as geitonogamy. In the genetic sense, geitonogamy is equivalent to autogamy (self-pollination occurring within one flower), except that the services of a pollinator are required (Faegri and van der Pijl, 1971).

The process of geitonogamy in Phacelias with congested inflorescences is well-described by Willis (1895), in a discussion of pollination in P. tanacetifolia.

> The dichogamy of the flower gives it some chance of cross-fertilization, especially as it is largely visited for honey and pollen; but it seems probable that self-fertilization is more common, even when it is visited by insects. The flowers are closely packed together...Insects crawl over the whole mass of flowers, touching stamens and styles indiscriminately, and probably often knock pollen on to the stigmas from the

> surrounding anthers...Every flower on the plants examined set a full complement of seed.

Heckard (1960) concurred with the observations of Willis, observing that, although self-pollination is probably common in the *Magellanicae*, "...it does not seem to occur to any extent when bees are lacking."

During the course of field studies, the action of insect visitors on *P. capitata* plants was observed. Their behavior was just as described by Willis (1895). Upon landing on an inflorescence, the insects would crawl over the entire "floral surface," collecting nectar (Dr. L. Macior, pers. comm.) from the flowers. It could be seen that in this process the stamens and styles of many flowers are pushed about, undoubtedly giving the opportunity for geitonogamy. Even autogamy is possible if some pollen remains on anthers long enough for stigmas of the same flower to mature. Insects were often observed moving from one inflorescence to another on the same individual. In particularly dense populations of *P. capitata* the plants are often so close together that inter-plant visitation by the same pollinator was also observed. In this way, there is an opportunity for cross-pollination as well, if pollen is retained on the body of the insect.

Cross-fertilization does occur in these plants, as evidenced by the instances of hybrid swarms and by interspecific intergradation at the tetraploid level, as observed by Heckard (1960). The suspected allopolyploid origin of certain tetraploid species, such as _P. hastata_, would require cross-pollination events as well.

In general, the pollination syndrome of _P. capitata_ is best described as facultatively xenogamous. Though geitonogamy is probably most frequent, opportunities for cross-pollination do exist. No evidence of apomixis in the _Magellanicae_ has been observed (Heckard, 1960).

Insects visiting several populations of _P. capitata_ and _P. corymbosa_ were collected during May, 1984, and were identified by Drs. J. Lattin, A. Moldenke, and W. Stephen of the Department of Entomology, Oregon State University. These potential pollinators are listed in Table 12. The most frequently observed visitors were bumblebees (_Bombus_ spp.) and the honey-bee, _Apis mellifera_. The variety of insect visitors found in this limited sample indicates a rather general, "open" pollination system for _P. capitata_. In a study of pollination ecology in California, Moldenke (1976) stated that _Phacelia_ species are heavily visited by both "specialist" and "generalist" vectors. The _Bombus_ species visiting _P. capitata_ and _P. corymbosa_ are generalists, while in one instance, an individual of _Melissodes_, ordinarily a genus of specialists visiting members of the family Asteraceae (Dr. A. Moldenke, pers. comm.), was found collecting nectar from _P. capitata_.

Seed production. _Methods_. To compare the extent to which _Phacelia capitata_ sets seed with and without natural pollinators available, five exclosures were established.

Table 12. Insect pollinators of *Phacelia capitata* and *P. corymbosa*.

Phacelia species	Order	Family	Genus and species
P. capitata	Hymenoptera	Apidae	*Apis mellifera* L.
			Bombus californicus Smith
			B. caliginosus Frison
			B. edwardsii Cresson
			B. huntii Greene
			B. vosnesenskii Rad.
		Anthophoridae	*Melissodes* sp.
		Megachilidae	*Osmia* sp.
	Lepidoptera	Lycaenidae	*Everes comyntas* Godart
P. corymbosa	Hymenoptera	Apidae	*Apis mellifera* L.
			Bombus vosnesenskii Rad.

These exclosures were set up in the Beatty Creek Research Natural Area on April 25, 1984. The fruiting inflorescences were retrieved on June 30, 1984.

The exclosures consisted of small milk carton sections which were placed in a short segment of nylon netting. The netting was tied off around the stem below the inflorescence; it was tied on the top to a stake, which supported the entire exclosure. All exclosures were established before the first flowers had opened.

Upon retrieving the exclosures, paired inflorescences from the same individuals, which had been left open to natural pollination, were collected. The number of flowers and seeds produced by the five inflorescence pairs were then counted.

Results. Seed production in open-pollinated and enclosed inflorescences is summarized in Table 13. There was no significant seed production in inflorescences that were excluded from pollinators. These results are in agreement with the observations of Heckard (1960), who noted that caged plants of *P. californica* produced only an occasional seed per cyme.

Although the data indicate that pollinators are needed for appreciable seed set in *P. capitata*, they do not provide information on the extent to which the flowers are self-pollinated or out-crossed; as previously stated, however, selfing is probably prevalent. Careful artificial self-pollination would be needed to determine the extent of

Table 13. Seed production in open-pollinated and enclosed inflorescences of *Phacelia capitata*.

Inflorescence*	Number of flowers	Number of flowers producing seed	Percent flowers producing seed	Number of flowers with evidence of seed predation	Number of flowers producing:		
					1 seed	2 seeds	3 seeds
1-1 open	158	61	38.6	18	55	6	0
1-1 closed	130	0	0.0	0	0	0	0
1-2 open	108	40	37.0	4	40	0	0
1-2 closed	136	0	0.0	0	0	0	0
2-1 open	247	175	70.8	20	85	87	3
2-1 closed	219	1	0.46	0	1	0	0
2-2 open	154	82	53.2	30	55	27	0
2-2 closed	154	5	3.3	0	4	1	0
3-1 open	59	49	83.1	0	49	0	0
3-1 closed	53	0	0.0	0	0	0	0

*-First number indicates individual plant; second number indicates inflorescence pair from each plant.

self-compatibility. Such hand pollinations are difficult in the field, owing to the congested inflorescences and small stigmatic surfaces; several attempts ended in the breaking of the stems. Heckard (1960) alludes to the difficulties in artificially self-pollinating plants in the complex. With few exceptions, artificial pollinations gave a low percentage of seed set compared to that obtained by natural pollinations.

Some seed predation occurs in inflorescences of _P. capitata_ (Table 13). In the cases where this was observed, small holes were present in the sides of the capsules, and no seeds had developed. No insects were found that could be implicated in this seed predation.

Pollen viability. _Methods_. A survey of pollen viability in populations of _Phacelia capitata_, _P. corymbosa_, _P. hastata_, and _P. heterophylla_ ssp. _virgata_ was made. The pollen grains were sampled from dried herbarium specimens. One to three dehisced anthers, all from a single flower, were used. The pollen was stained with cotton blue in lactophenol, and counts were made using a Zeiss light microscope.

Results. The pollen viability counts are listed in Table 14.

The degree of pollen viability is often useful as a conservative indicator of the fertility of individuals. For example, reduced pollen viabilities may characterize sterile hybrids resulting from interspecific crosses.

Table 14. Pollen viability in _Phacelia_ species group _Magellanicae_.

Species	Population	n	Number of pollen grains examined	Percent viable pollen	Collection
P. capitata	Bilger Creek	11	480	95	Shelly & Nelson 724
	Boomer Hill I	11*	758	93	Shelly & Holmes 769
	Boomer Hill II	11	572	58	Shelly & Holmes 781
	Bridge	11*	593	95	Shelly & Nelson 754
	Callahan Creek	22*	583	98	Shelly & Nelson 733
	Cow Creek I	11*	645	97	Shelly 709
	Cow Creek II	11*	710	92	Shelly 412
	Cow Creek Turn-off	11*	802	85	Shelly 719
	Doe Creek	11	817	86	Shelly 706
	Doe/Thompson Ridge	?	526	99	Shelly & Holmes 783
	The Drew	11*	516	98	Shelly & Nelson 734
	Elk Creek	11	710	71	Shelly & Nelson 726
	Goolaway Gap	11*	865	98	Shelly & Nelson 737
	Little River	11*	198	93	Shelly 349
	Myrtle Creek North	11*	761	96	Shelly 721
	Rice Creek	?	813	80	Shelly & Holmes 792
	Salt Creek	11*	223	71	Shelly & Nelson 725b
	Weaver Road	11*	687	65	Shelly 720
P. corymbosa	Eight Dollar Mtn I	22	447	45	Shelly 700
	Eight Dollar Mtn II	22	579	96	Shelly 702
	Rough & Ready	22	552	97	Shelly 698
	Waldo	22	418	81	Shelly 697
	Wimer Road	22*	568	36	Shelly 691
P. hastata	Boomer Hill I	22	1703	49	Shelly & Holmes 767
P. heterophylla	Elk Creek	11*	538	96	Shelly & Nelson 727

*-Pollen viability obtained from a specimen other than the chromosome count voucher.

Thus, viability counts may be of use in studying known or suspected intergradient populations and in assessing the degree of interfertility between species or populations. In this project, it was hoped that pollen viability could be used to study the potential hybrid nature of the *P. capitata* populations containing tetraploids (Elk Creek and Callahan Creek), and to describe the range of variation in pollen viability among diploid populations of the species.

The results are inconclusive. Although plants from diploid populations of *P. capitata* generally show the high percentage of viable pollen expected in nonhybrids, there are four exceptions (Boomer Hill II, Elk Creek, Salt Creek, and Weaver Road) in which pollen viability of diploids is severely lowered (i.e., less than 75%). In addition, both high and low pollen viabilities were found in plants from tetraploid localities of *P. corymbosa*. Due to this variability in nonhybrid diploid and tetraploid populations, pollen viability is of limited usefulness as an indicator of hybrid origin in the tetraploid *P. capitata* populations.

Environmental factors may strongly influence pollen viability. Heckard (1960) found that in nonhybrid species of the *Magellanicae*, high pollen viability was always observed, but that "...a variation of about 10 percent can be attributed to the environment." In an extreme case involving studies of *P. californica* and *P. imbricata*, he found that pollen viability varied within the same populations depending on when they were sampled. Heckard concluded that the increasing pollen abortion observed through the blooming period was "...largely a result of a decrease in available water and an accompanying decrease of vigor." Such environmental variations, perhaps including temperature fluctuations, may have contributed to the variability in pollen viability observed in this study.

Competitive ability and ruderal response

The hypothesis that certain species are limited to serpentine soils, not only as a result of possible physiological restrictions to such habitats but also because of poor competitive ability in more closed communities of non-serpentine substrates, has been offered by several botanists. Kruckeberg (1951), in studies comparing growth of plant species found on and off serpentine soils, concluded that the superior growth of all the species tested on non-serpentine soil suggests that "...the serpentine endemics are not restricted to serpentine merely because of some specific requirement uniquely provided by serpentine." In a later report (Kruckeberg, 1954), he again suggested that, because growth of serpentine plants was found to be better on non-serpentine than on serpentine soils, some other factor aside from chemical tolerance must be sought to explain serpentine restriction. He postulated that the serpentine endemics are unable to maintain themselves against the rigorous competition of non-serpentine plant communities. Stebbins and Major (1965) agreed, stating that "...serpentine endemics are preserved from extinction by the ability to grow on serpentine where more competitive plants cannot grow."

Phacelia _capitata_ appears to provide an excellent example of a serpentine endemic with poor competitive ability. A greenhouse germination test on non-serpentine soil showed that the species has the ability to germinate and grow on non-ultramafic soils (80% germination rate). However, _P_. _capitata_ is not found off serpentine soils (or a possibly close metamorphic derivative thereof, i.e., at the Boomer Hill I site) in nature. The following field observations indicate that the serpentine restriction of the species may be a result, in part, of the species' apparently poor competitive ability, evident even in its own native, undisturbed habitat.

In undisturbed serpentine communities, _P_. _capitata_ is often found in very specific types of microsites. On the serpentine slopes at the Peel site, individuals occur frequently along intermittent, vernally scoured stream channels in which cover of other species is low. The plants which occur in these shallow channels are often very large, as well. In the surrounding vegetation, where cover of annual grasses and other forbs is higher, the frequency of _P_. _capitata_ is noticeably less.

The apparently poor competitive ability of the species, again within its own undisturbed native community, is also evidenced on the serpentine slopes along Beatty Creek. Here, individuals are widely scattered and infrequent throughout the herbaceous layer of the *Pinus jeffreyi* savanna. However, in instances where large outcrops of serpentine bedrock occur, *P. capitata* plants are frequent in the cracks of the rocks. In addition, an interesting example which suggests the need for a very open "safe site" for good seed germination was observed here. In a location where a dead *Pinus jeffreyi* trunk had fallen over, a large hole was left in the soil by the upturned root mass. This hole contained seven large, floriferous *Phacelia capitata* individuals, while in the surrounding herb layer, very few plants, and no other such concentrated "clumps," were found.

Owing to the apparent requirement for lowered competition, perhaps in the seed germination and establishment phases, one might expect *P. capitata* to invade and grow well in disturbed areas. Indeed, such is the case--at all 18 sites where some disturbance of the serpentine soil has occurred, *P. capitata* is noticeably more abundant on the open, barren areas (i.e., roadbanks, rock quarries, etc.) than in the surrounding, undisturbed serpentine habitat.

Quantitative data to illustrate this ruderal response were collected at Lee Creek, on a serpentine hillside traversed by a logging road. Seven 4x4 m square plots were set up: three plots on the barren roadbank, three plots located five meters above the uphill edges of the roadbank plots in undisturbed vegetation, and one plot on an adjacent bedrock outcrop. The results are given in Table 15. The data show that P. capitata individuals are more numerous, and have a higher percent cover, on the exposed outcrop compared to adjacent undisturbed areas where cover of other species is higher. The plants are most abundant, however, on the raw serpentine roadbanks where percent cover of other species is lower. Also of interest is the fact that the only seedlings observed (i.e., with cotyledons still apparent) were in two of the roadbank plots.

It would be naive to conclude, on the basis of these field observations alone, that competitive exclusion is the single, or even the most important, cause of the serpentine restriction of P. capitata. The situation may be much more complex, and more controlled experiments would be necessary to fully understand the autecology of the species.

As an example, the growth rates of P. capitata on serpentine and normal soils could be compared, to determine whether the species grows optimally on ultramafic soils which have ordinarily toxic concentrations of certain elements, such as magnesium. Also, Grime (1979) summarizes evidence indicating that, in instances where plants associated with nutrient-deficient habitats such as serpentine soils were supplied with high rates of mineral

Table 15. Ruderal response of *Phacelia capitata* at Lee Creek. Data collected from seven 4x4 m plots.

Plot	Number of plants (non-flowering; flowering)	Percent cover	Number of seedlings	Percent cover of other vegetation		
				Herbs	Shrubs	Trees
A. Roadbank plots						
1	0; 28	8.0	5	1.5	0.0	0.0
2	14; 31	5.0	1	2.0	1.0	10.0
3	3; 24	25.0	0	1.0	0.0	0.0
B. Undisturbed plots						
4	4; 4	1.5	0	55.0	0.0	15.0
5	0; 0	0.0	0	95.0	0.0	75.0
6	1; 0	0.1	0	90.0	0.0	70.0
C. Rock outcrop plot						
7	5; 9	2.0	0	8.0	0.0	0.0

nutrients (i.e., calcium), these nutrients appeared to be accumulated in quantities detrimental to the growth of such plants. Perhaps P. capitata provides such an example, in which there is a "requirement" for the low concentrations of phosphorous and calcium which probably characterize many of its sites. Of course, the possibility that special soil requirements and poor competitive ability may operate together also exists. Lack of required soil properties, in this case on non-serpentine substrates, may lower the competitive ability of a serpentine endemic such as P. capitata on such soils. Lastly, P. capitata may be a good example of a "stress-tolerator" (Grime, 1979), in that it naturally exists in habitats characterized by high stress (i.e., poor soil nutrient status) and light disturbance. If so, then the intrinsically slower growth rate which is generally characteristic of such species may also decrease the competitive ability of this and other serpentine endemics.

Thus, as Kruckeberg (1954) and Proctor and Woodell (1975) state, the full nature of the competitive exclusion hypothesis, which may be so important when considering the ecology and evolution of serpentine endemics, remains unknown. Clearly this is a fertile area for research, and Phacelia capitata may provide a very revealing subject.

DISCUSSION AND CONCLUSIONS

Speciation and evolutionary relationships

The *Phacelia magellanica* alliance (species group *Magellanicae*) provides an example of a mature polyploid complex. In such complexes, both the morphological and ecological extremes are usually represented by the diploid species. However, the diploids are often less common than the polyploids. Their geographic ranges are more restricted, and the amounts of genetic variation within their populations is usually less. In addition, the diploids are usually allopatric with each other, or sympatric only in restricted areas, so that the likelihood of hybridization and doubling of chromosome number involving different diploids is much reduced (Stebbins, 1971).

Of the six species of the *Magellanicae* that occur almost exclusively or partially as diploids, two have been considered in detail in this study: *P. capitata* and *P. corymbosa*. Each of these is a good example of a "morphological and ecological extreme," having very distinct morphological characteristics and special ecological attributes in the form of virtually complete restriction to serpentine soils. Of all six species which occur as diploids in the *Magellanicae*, however, *P. capitata* is the most restricted in its geographical range. Thus, its morphological distinctiveness, restriction to serpentine soils (or a close derivative), narrowly endemic distribution pattern, and almost exclusive occurrence at the diploid level make _P_. _capitata_ an unusual, unique entity in the _Magellanicae_.

It is difficult to elucidate the evolutionary history of such a diploid in a mature polyploid complex, but speculation is interesting. In considering possible modes of speciation for _P_. _capitata_, it is convenient to consider two types of endemic species, which differ in their origins: insular and depleted endemics. Insular endemics are those which never were common, but which diverged from a small group of individuals of a widespread ancestral species, following the establishment of these individuals upon a small, isolated area. Depleted species are those which were once more common, widespread, and richer in biotypes (genetically different populations), but whose present rarity is due to depletion of genetic variability through subsequent loss of biotypes (Stebbins, 1942a).

These two types of restricted species may be further distinguished from one another by two criteria. First, if an endemic is closely related to widespread species which occur in surrounding continental areas, it is probably a strictly insular species; if it is closely related to no other living form, it is more likely a depleted species. Secondly, if the endemic is morphologically a highly specialized form compared to its relatives, it is probably an insular descendent of these, while if it is less specialized it may be a depleted ancestor (Stebbins, 1971).

Based on observations regarding the cytology, competitive ability, edaphic restriction, geographic distribution, and morphological characteristics of *Phacelia capitata*, and theories regarding the origins of modern-day vegetation in the Klamath Mountains, one can support, without much difficulty, an insular mode of origin for this species.

In polyploid complexes found in nature, the members with the lowest number of chromosomes are the primitive ones, while the polyploids are derived from them (Stebbins, 1942b). In addition, polyploidy is predominantly an irreversible trend from lower to higher levels (Stebbins, 1971). Thus, at least the direction of evolution in complexes such as the *Magellanicae* can be known, and divergence and speciation at the diploid level will have formed the initial, primary mode of evolution for such groups. Because *P. capitata* occurs almost exclusively as a diploid, it can be concluded that the evolutionary events leading to the origin of the species occurred at this chromosome level. This being the case, then *P. capitata* can be described as one of the evolutionary "offshoots" from the ancestral diploid stock which formed the foundation of the *Magellanicae*.

The northward migrations of elements of the Madro-Tertiary Geoflora probably brought with them, sometime since the beginning of the Pliocene epoch, the ancestral *Phacelia* species from which *P. capitata* evolved. This correlates well with the conclusion of Stebbins (1971) that the majority of polyploid complexes that may presently be considered mature probably originated during the Pleistocene or Pliocene epochs, between approximately 500,000 and 10,000,000 years ago. Upon the ancestral species' contact with the serpentine substrates in California and southwestern Oregon, the process of natural selection for a few, perhaps partially preadapted, serpentine-tolerant individuals could have begun. Further divergence may have ended with the "insular" isolation of *P. capitata* on the serpentine outcrops which it presently occupies.

The fact that *P. capitata* possesses poor competitive ability not only provides one possible explanation for the species' present restriction to serpentine soils, it also helps explain the hypothetical evolutionary history of the species. If the few individuals which were developing serpentine tolerance were only able to survive and reproduce in the more open communities on serpentine soils, this could reinforce the selection for serpentine tolerance, and further divergence of the individuals giving rise to the species could occur. The persistence of *P. capitata* through time, despite poor competitive ability, thus may be owed to its ability to tolerate the chemically imbalanced soils, and to its consequent "escape" of the rigors of competition. The morphological distinctness of *P. capitata* from other widespread members of the *Magellanicae*, as well as its restricted geographic distribution, provide further evidence that the species is an insular endemic.

The cytogeography of *Phacelia corymbosa*, a related species which replaces *P. capitata* on ultramafic soils to the south, is also of interest when considering a possible mode of origin for the latter species. Figure 8 illustrates the allopatric distribution pattern of these species in Oregon. It is logical to speculate that, because both species are largely restricted to serpentine soils, they may share a common ancestor. Two problems make this a difficult hypothesis to substantiate. First, *P. corymbosa* is not known to occur as a diploid in Oregon, as discussed previously. The northernmost known diploid location for *P. corymbosa* is in Siskiyou County, California, approximately 175 km south of the southernmost location of *P. capitata* (Heckard, 1960). Second, the two species are both distinct morphological entities in the *Magellanicae*, and they are very different from one another. If a common diploid ancestor was in fact shared by the two species, it must surely have been long extinct. No evidence for any present genetic interaction between *P. capitata* and *P. corymbosa* was found.

Even the study of a morphologically distinct, narrowly restricted endemic such as *P. capitata* has not been spared the difficulties of polyploidy and interspecific

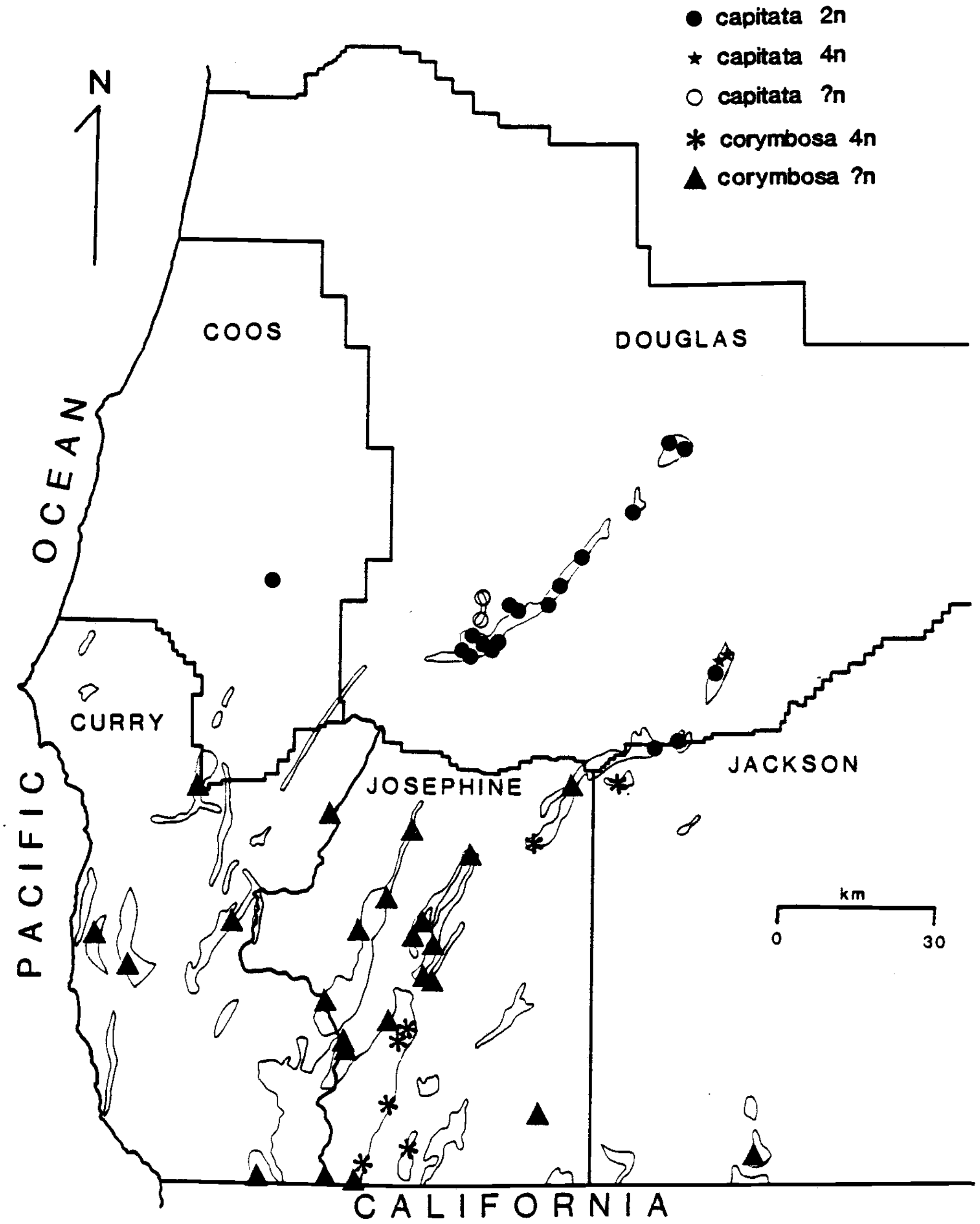


Figure 8. Distribution of Phacelia capitata and P. corymbosa in southwestern Oregon. Ultramafic formations outlined (Wells and Peck, 1961). Phacelia corymbosa locations are plotted from herbarium specimens, except for the tetraploid location at Sexton Mountain, Josephine County (Heckard, 1960).

hybridization. As Jackson (1976) states, the "...attainment of polyploidy by a taxon and its later interaction with diploids and other polyploids may cause ...confounding factors not encountered in diploids." Further, he states that caution is necessary in "...interpreting the variation of tetraploids in one place as due to introgression from local diploids or other tetraploids." Stebbins (1971) concluded that this may be due to the fact that the morphological criteria used by taxonomists are inadequate guides to the evolutionary origin of many such tetraploid populations. With these limitations in mind, the interrelationships of *P. capitata* within the *Magellanicae* may be considered.

Certain of the early collections of *Magellanicae*-type *Phacelias* in Douglas County, Oregon (see Taxonomic Relationships), which Kruckeberg (1956) likened to *P. capitata*, are suggestive of former genetic interrelationships of the species with other members of the complex, especially *P. hastata*. These collections may represent intergrades between these two species, but most are at this time best referred to the widespread, variable *P. hastata*. The specimen collected by Constance and Rollins (2956, DS) is the most intermediate in appearance. Although Heckard (pers. comm.) felt this plant may combine genomes of *P. capitata* and *P. corymbosa*, it lacks the conspicuous, intermediate-length glandular trichomes of the latter which would be expected in such a hybrid. On this basis, and because the area near Mt. Nebo where this specimen was found is not on serpentine soil, it is most easily referable to _P_. _hastata_, with a note as to possible affinities with _P_. _capitata_. I have found the former species to be extant in the Mt. Nebo area.

A site which is potentially revealing with respect to species intergradation is the Boomer Hill I site. This is the only location where _P_. _capitata_ was found in biotic sympatry with another member of the complex (_P_. _hastata_). Chromosome counts of individuals representing "good" examples of each species showed that the former species occurs as a diploid and the latter as a tetraploid, a situation which ordinarily limits the possibility of hybridization between species. Some collections (_Shelly_ _&_ _Holmes_ _768_, _771_) appear to be intermediate, however, in their possession of relatively narrow, predominantly entire, silvery leaves. Attempted chromosome counts on these intermediate specimens were unsuccessful, as all the buds were past meiosis. On the basis of other features, however, the occurrence of hybridization between _P_. _capitata_ and _P_. _hastata_ can at least be postulated. Of interest at this site is the less stringent nature of the soil, which is intermediate between the highly serpentinized habitats to which _P_. _capitata_ is largely restricted, and a more normal soil chemical profile. This, plus the disturbed nature of the roadside habitat, are perhaps the factors which have allowed _P_. _hastata_ and _P_.

capitata to become sympatric here.

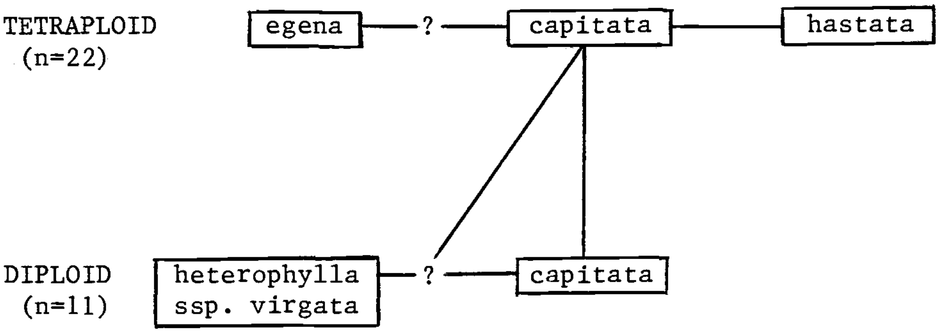
The populations of *P. capitata* containing tetraploids are further examples of the problems involved in determining origins of such individuals. The Elk Creek population is a mixture of diploids and tetraploids, while at the Callahan Creek population, only a tetraploid count was obtained. It may be best, in seeking to describe the significance of these two sites, to realize that they are in neighboring sympatry, occurring within approximately 0.8-1.0 km of each other. The presence of tetraploid individuals at both of these sites may therefore be related to a single polyploidization event (i.e., hybridization followed by chromosome doubling) in the past.

On the basis of field observations, the most likely other diploid parent for these intergradient populations appears to be *P. heterophylla*. This species is neighboringly sympatric with *P. capitata*, occurring along the highway both north and south of the serpentine outcrops above Elk Creek. In surveys throughout the vicinity, no other morphologically distinct members of the *Magellanicae* were found. Highly variable, possibly tetraploid individuals of *P. capitata* are not restricted to the disturbed roadbank at this location, but occur in undisturbed serpentine areas above the road as well. This suggests that the possible hybridization event which led to the polyploidization of *P. capitata* occurred prior to habitat disturbance in the area, the tetraploids having since colonized the roadbank.

With respect to the Elk Creek population, Heckard noted on his collection (2930, JEPS) the possibility that P. capitata may have interacted with a Californian member of the Magellanicae, P. egena. The occurrence of this species in Oregon, and its morphological characteristics here, are too poorly known at this time to allow any strong conclusions along these lines. It is feasible that the larger corollas and leaf lobing patterns of P. capitata at Elk Creek could have resulted from hybridization in the past with either a species similar to P. egena or with the locally sympatric P. heterophylla. Long-term introgression involving the tetraploids and diploids at this site may have so obscured the hybrid nature of the plants that exact determination of their origin is not possible. Only lengthy field and artificial hybridization studies could perhaps offer answers to the origin of these populations.

Figure 9 summarizes the possible interrelationships of P. capitata within the Magellanicae. In the face of the complications discussed above, it is appealing to interpret the occurrence of limited interspecific gene exchange as "evolutionary noise," when one considers the distinctive patterns of morphological, ecological, and almost complete cytological isolation of P. capitata within the complex in southwestern Oregon.

Figure 9. Possible interrelationships of *Phacelia capitata* within the species group *Magellanicae*.



The endemic status of the species

Although the classification of endemic species has traditionally been very complex, two extreme types, neoendemics and paleoendemics, have formed the basis for discussions of endemism since the late 1800s. Neoendemics represent "new" taxa which have evolved in a particular area from which they have not yet spread. Paleoendemics are taxa which once possessed much wider distributions but which are now confined to a very limited portion of their former range (Stebbins and Major, 1965; Stott, 1981).

A third category, the holoendemic, has also been described, which is intermediate in character between the above extremes. Such a species, even when covering its maximum area, is still narrowly restricted, most often by virtue of physical or physiological (ecological) barriers (Richardson, 1978). The characteristics of the three endemic categories with respect to various attributes are summarized by Richardson as follows:

Attribute	Endemic status			
	Neo-	Holo-	Paleo-	*P. capitata*
taxonomically isolated	-	-	+	-
geographically isolated	-	+	+	-
polymorphic	-	+	-	-
derived characters	+	+	-	+?
environment stable	+/-	-	+	+
ploidy level high	+/-	+/-	(+)/-	-
potential to expand area	+	+/-	-	+?
age (recent +, old -)	+	+/-	(+)/-	+

As he makes clear, there are many exceptions to the attribute states, and there is no clear distinction between the three types.

Since *P. capitata* is geographically and ecologically restricted to a small area, and surely did not once occupy a much larger area, it is not a paleoendemic. It is, however, not clear if the species is best characterized as a neo- or holoendemic; it seems to most closely fit the former category. The possibility of *P. capitata* expanding its range to the serpentine areas south of its present distribution seems logical, unless there are unknown soil chemical, climatic, or other factors which might prevent this. The analyzed soils occupied by *P. capitata* and *P. corymbosa* are quite similar in chemical nature.

According to Stebbins (1971), endemics which are localized in specialized habitats in regions such as western North America, and have close relatives of more generalized distribution in the surrounding vegetation, must be of recent origin. This, too, supports the classification of *P. capitata* as a neoendemic.

Thus, the most reasonable interpretation of *Phacelia capitata* may be to classify it as an insular neoendemic.

Recommendations for preservation

Endemic taxa such as *Phacelia capitata* are of great scientific interest and value. As a consequence of their restricted geographical distributions and often specialized ecological requirements, they are also most likely to become endangered as a result of habitat modification or destruction. It is imperative that such species be studied and documented before they are lost to extinction.

Phacelia capitata presents a paradoxical case for a serpentine endemic, since habitat disturbance has led to an increase in the abundance of the species. Thus, at least at this time it is not appropriate to consider the species "endangered" with extinction. Most recently, the species was placed on the "watch list" of Oregon rare, threatened, and endangered plant species, after being removed from a list of taxa threatened throughout their range (Oregon Natural Heritage Data Base, 1985). In addition, it has been recommended for removal from candidacy as a threatened species under the Federal Endangered Species Act of 1973.

The geographically narrow serpentine restriction of the species does provide a basis for maintaining *P. capitata* on a "watch list." In this way, its populations can be monitored to detect any decline in numbers which may occur with further destruction of its habitat, such as by increased mining of the serpentine substrates. Its weedy tendency in disturbed areas has, for the time being, allowed for the persistence of this unique species. It is still important, however, to protect undisturbed populations of such species, so that features of their population ecology, habitat requirements, and evolutionary uniqueness may be studied in natural settings.

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APPENDIX

APPENDIX

Specimens cited (in addition to those discussed in the Taxonomic Relationships section):

Phacelia capitata Kruckeberg. OREGON: Coos Co.: N of St. Hwy. 42, 3.2 km E of Bridge, 100 m, *Kruckeberg 2703* (WTU, isotype), *Sundberg 1031* (OSC), *Shelly & Nelson 754* (OSC). Douglas Co.: Beatty Creek, 0.4 km N of Cow Creek Road, 320 m, *Shelly 419* (OSC); BLM rd. 29-5-11.0, 2.3 km NW of Bilger Creek Road, 490 m, *Shelly & Nelson 724* (OSC); Boomer Hill Road (BLM rd. 30-6-4.2), 8.1 km SW of Interstate Hwy. 5, 760 m, *Shelly & Holmes 766*, *769* (OSC); BLM rd. 30-6-4.1, 0.5 km from BLM rd. 29-6-34.0, 850 m, *Shelly & Holmes 781* (OSC); Callahan Creek, Umpqua NF rd. 3230, 0.5 km W of St. Hwy. 227, 490 m, *Fosback s.n.* (OSC), *Shelly 440* (OSC), *Shelly & Nelson 733* (OSC); Cow Creek Road, 0.5 km W of Doe Creek Road, 300 m, *Shelly 405*, *709* (OSC); NW side of Cow Creek, 1.2 km SW of Doe Creek Road, 300 m, *Shelly 411*, *412* (OSC); Cow Creek Road, 4.8 km W of Glenbrook Loop Road, 230 m, *Shelly 681*, *719* (OSC); Doe Creek Road, 1.9 km N of Cow Creek Road, 400 m, *Shelly 706* (OSC); BLM rd. 30-7-14.0, 3.2 km NW of Doe Creek Road, 640 m, *Shelly & Holmes* 783 (OSC); The Drew, 810 m, *Shelly & Nelson 734* (OSC); Elk Creek, along St. Hwy. 227, 1.6-4.0 km SE of Tiller, 375 m, *Heckard 2930* (JEPS), *Shelly 433* (OSC), *Shelly & Nelson 726* (OSC); Lee Creek, BLM rd. 28-4-15.0, 415 m, *Fosback et al. s.n.* (OSC), *Shelly 399* (OSC); Little River, 5.9 km SE of Glide, 270 m, *Parker & Parker s.n.* (OSC), *Shelly 349*, *690* (OSC);

Co. Rt. 14, 1.6 km NW of Myrtle Creek, 245 m, *Howell 28807* (CAS), *Shelly 414*, *721* (OSC); Nickel Mountain, ca. 365 m, *Detling 6339* (ORE); BLM rd. 26-3-34.2, 0.5 km E of Peel, 295 m, *Knouse & Moore s.n.* (OSC), *Shelly 354* (OSC); SW flank of Red Mountain, 930 m, *Detling 5314* (ORE), *Shelly & Nelson 736* (OSC); Rice Creek, BLM rd. 29-7-36.0, 710 m, *Shelly & Holmes 792* (OSC); Salt Creek, BLM rd. 30-7-36.0, 340 m, *Shelly & Nelson 725*, *725b* (OSC); Weaver Road, 2.9 km SW of Interstate Hwy. 5, 210 m, *Ornduff s.n.* (JEPS), *Shelly 689*, *720* (OSC). Jackson Co.: Goolaway Gap, 930 m, *Shelly & Nelson 737*, *738* (OSC).

P. corymbosa Jepson. OREGON: Jackson Co.: Grave Creek Road, 3.5 km N of Slate Creek Road, 850 m, *Shelly 441* (OSC). Josephine Co.: Eight Dollar Mountain, Siskiyou NF rd. 4201 at Illinois River, 390 m, *Shelly 700* (OSC); Eight Dollar Mountain, Deer Creek, 5 km W of Selma, 450 m, *Shelly 702* (OSC); Rough and Ready Botanical Wayside, 8 km S of Cave Junction, 425 m, *Shelly 698* (OSC); Waldo, 4.2 km E of O'Brien, 475 m, *Shelly 697* (OSC); Wimer Road, 6.5 km SW of O'Brien, 490 m, *Constance & Bacigalupi 3394* (WTU), *Shelly 691* (OSC).

P. hastata Douglas ex Lehmann. OREGON: Douglas Co.: Boomer Hill Road (BLM rd. 30-6-4.2), 8.1 km SW of Interstate Hwy. 5, 760 m, *Shelly & Holmes 767*, *768*, *771* (OSC).

_P_. _heterophylla_ Pursh ssp. _virgata_ (Greene) Heckard. OREGON: Douglas Co.: Cow Creek, 0.1 km W of Doe Creek Road, 300 m, _Shelly_ _714_ (OSC); Elk Creek, along St. Hwy. 227, 0.8 km E of Tiller, 350 m, _Shelly_ _&_ _Nelson_ _727_, _728_ (OSC).