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A preliminary survey of the concentration of selected ions in some California native plants growing in serpentine and non-serpentine soil

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A Preliminary Survey of the Concentration of Selected Ions

in Some California Native Plants Growing in

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by

Gregory Roger Boyko

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INTRODUCTION

"In varying degrees, plant life on ultramafics
[serpentine soil] all over the world casts the
same spell, conjures the same bleak images, and
excites the analytical mind" (Kruckeburg, 1969,
in Proctor & Woodell, 1975: 265).

Anyone driving through the foothills of the Sierra Nevada of
California has observed the sudden change in the landscape from rel-
atively abundant vegetation to a sparseley vegetated, barren-appearing
soil dominated by a few species of "tough-looking" plants. These are
areas of serpentine soil. The apparent sterility of these soils is even
more striking because they are often adjacent to fertile agricultural
land, but are themselves unsuited to almost any type of agriculture
(Proctor & Woodell, 1975).

The serpentine soils of California occur primarily in the
Sierra Nevada foothills where magnesium-rich rock intruded through the
original strata. These intrusions became serpentenized and through
weathering gave rise to the present soils (Taliaferro, 1943).
Technically "serpentine" refers to a small group of minerals of similar
chemical composition which are products of hydrothermal alteration.
The essential mineral is olivine, $(MgFe)_3SiO_4$, or its hydrated form,
serpentinite, $H_4(MgFe)_3SiO_9$. By convention biologists use the term
serpentine for any rock rich in ferromagnesian minerals, and the term is
not intended as a precise mineral description (Proctor & Woodell, 1975).
The only generalization that can be made is that such rock is rich in
iron and magnesium and low in silicon. It is usually low in calcium,
potassium, phosphorus and molybdenum and rich in nickel, chromium and

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cobalt. The soil which results from the weathering of these rocks will have varying chemical compositions depending upon a large number of factors (total amount of rainfall, chemical composition and pH of the rain, temperature, drainage and slope) interacting with the specific chemical composition of the original rock. As a result of weathering, the resultant soil may differ markedly from that of the rock from which it was derived, and may differ between closely adjacent localities (Lyon, et al., 1970; Proctor & Woodell, 1975).

Typically these soils have sparse plant cover with much surrounding barren ground. They may harbor rare species endemic to one or a few serpentine outcrops, but a wide variety of plants are able to survive on both serpentine and non-serpentine soil (Kruckeberg, 1969, in Proctor & Woodell, 1975). There is a large percentage of xeric forms and stunting is characteristic, presumably due to the lack of water holding capacity of the soil and abnormal ion balances. Serpentine soils in different parts of the world show different ion imbalances, but in general these soils show "low levels of nitrogen, phosphorus and potassium; low calcium and a high level of magnesium giving an unfavorable calcium/magnesium balance; low molybdenum, relatively high nickel, chromium and cobalt" (Proctor & Woodell, 1975: 271). There have been many suggestions about the reason for lack of vegetation in serpentine soils. Soil chemistry is critical (Kruckeberg, 1969, in Proctor & Woodell, 1975), but whether the major factor is the calcium/magnesium ratio, low nutrient level or high concentration of toxic trace elements seems to depend on the particular serpentine soil being studied (Lyon, et al., 1971; White, 1971; Slingsby & Brown, 1977; Rundel & Parsons, 1980).

All vascular plants show some selection in the uptake of substances from soil by accumulation and exclusion of specific ions. Several studies have analyzed the relative concentrations of significant ions in serpentine endemics (Lyon, et al., 1970, 1971; Shewry & Peterson, 1975, 1976; Rundel & Parsons, 1980) and suggested mechanisms by which these plants survive under what would ordinarily be considered unfavorable circumstances. Some of these not-mutually-exclusive mechanisms include changes in root morphology, cationic uptake, translocation of nutrients and interaction between nutrient cations (Main, 1974).

Most of the reports on ion differences between plants growing on serpentine and non-serpentine soils have been for agriculturally important species (Madhok & Walter, 1969; Jones, et al., 1976; Marrs & Proctor, 1976; Wallace, et al., 1977) or serpentine endemics (Proctor & Woodell, 1975). Proctor & Woodell's comprehensive monograph includes a long list of papers on serpentine endemics from all parts of the world. However, there is almost no information on non-endemic species living in both serpentine and non-serpentine areas.

Do the peculiar ion concentrations of serpentine soils appear in the tissues of plants growing on those soils? To what extent are the same species of plants growing in serpentine and non-serpentine soil similar in ionic concentrations? This work was an attempt to answer these questions.

MATERIALS AND METHODS

Sample Collection

Leaf and stem portions of eight species of native California

plants and samples of the soil on which they were growing were collected

from serpentine and non-serpentine areas of California (Fig. 1). All

specimens of each species were collected at a single location for

serpentine and a single location for non-serpentine. Species collected

were: Clarkia biloba, Plantago hookeriana, Mimulus guttatus, Eremocarpus

setigerus, Asclepias fascicularis, Adenostoma fasciculatum, Heteromeles

arbutifolia and Pinus sabiniana (Appendix). Plants were collected while

in bloom to facilitate identification. Identifications were verified

by Dr. Dale McNeal, Department of Biological Sciences, University of the

Pacific, Stockton, California.

The entire aerial portion of the annuals and herbaceous

perennial and branch tips (10-15 cm) of the shrubs and tree were collected.

Immediately after collection, any adherent dust removed by shaking and

remaining stems, leaves and flowers air dried at 32 - 38°C. The dry

plant tissue was then pulverized into a coarse powder in a blender.

Soil was collected by removing leaf litter or surface roots to

a depth of 2-3 cm and a portion of soil removed which included approxi-

mately equal amounts from all depths between the initial near surface

to 25 cm. Soil samples were oven dried at 60°C for three days. The dry

soil was then ground to a powder of 20-30 mesh and sifted through a 32

mesh screen (U. S. A. Standard Testing Sieve meshes) to remove stones

and pebbles. (This grinding and sifting was done by Mr. Jack Schimasaki

of Nelson Laboratories, Stockton, California).

Laboratory Procedures for Plant Analysis

Six one-gram samples of dry material from each species from serpentine and six from non-serpentine were placed into clean, dry, pre-weighed crucibles, (all weighings were done on a Mettler, model H 15 balance) and ashed according to the method of Johnson & Ulrich (1959). This method requires adding enough of a solution of 5% sulfuric acid in 95% ethyl alcohol to each crucible to saturate the dry material and then igniting the mixture with a bunsen burner to produce a preliminary ash. The sulfated ash so obtained has less tendency to fuse to the crucible at higher temperatures and thus prevents loss of some of the elements.

Each sample was then placed in a cold electric muffle oven (Blue M, Muffle Furnace; Model No: M15A-1A) and heated to 500-550°C for six hours.

After formation of a carbon-free ash (uniform light grey color), the crucibles were removed from the oven, cooled and weighed.

The ashed material was then moistened with a small amount of water (4-5 drops) and 5 ml of 3 N hydrochloric acid was added. The acidic ash solution was poured into 50 ml Erlenmyer flasks and warmed on a steam bath for approximately 30 minutes to ensure that all salts except silica were in solution. After heating, approximately 20-30 ml of deionized water were added and the solution brought to 50 ml in a volumetric flask. This solution was filtered (Whatman #1) into a poly-propylene storage bottle as the stock solution for ion analysis by atomic absorption (Perkin-Elmer, 303). Ions analyzed were calcium, magnesium, sodium, potassium, chromium, and nickel in plants, soil and water.

Soil Analysis

Three one-gram samples of powdered soil from each location were weighed and placed into a 50 ml Erlenmyer flask with boiling chips and 15 ml of aqua-regia (3 parts concentrated hydrochloric acid to 1 part concentrated nitric acid). This solution was boiled slowly (1/2 to 1 hour) to a volume of 3-5 ml. After cooling, 35-40 ml. of deionized water was added and the solution boiled for 15 minutes, cooled, brought to 50 ml in a volumetric flask and stored in poly-propylene bottles for ion analysis by atomic absorption.

Pond Water Analysis

Two water samples were taken from near the surface of a permanent stock pond (surface area about 10 acres) located in a serpentine soil area, 4.5 miles N. E. of Ione on Hwy 124 (Fig. 2). Ion concentrations in the water were measured by atomic absorption (Perkin-Elmer, 303).

Figure 1. Map of plant and soil collection sites.

1. 1.7 miles east of Milton on Rock Creek Road. Non-serpentine soil. Eremocarpus setigerus.

2. 3.0 miles east of Milton on Rock Creek Road. Non-serpentine soil. Heteromeles arbutifolia.

3. 4.5 miles east of Milton on Rock Creek Road. Non-serpentine soil. Clarkia biloba.

4. 1.5 miles north of highway 108-120 on Tulloch Road. Non-serpentine soil. Mimulus guttatus.

5. 0.1 mile west of J59 on highway 108-120. Non-serpentine soil. Pinus sabiniana.

6. 1.0 mile south of highway 120 on Sims Road. Serpentine soil. Mimulus guttatus.

7. 2.5 miles south of highway 120 on Sims Road. Serpentine soil. Clarkia biloba, Plantago hookeriana, Asclepias fascicularis, Heteromeles arbutifolia and Pinus sabiniana.

8. 2.0 miles south of highway 49 on Marshes Flat Road. Non-serpentine soil. Plantago hookeriana.

9. On highway 49, 2.6 miles south-east of the junction of highway 120 and highway 49. Non-serpentine soil. Asclepias fascicularis.

10. On highway 49, 4.0 miles south-east of the junction highway 120-49. Non-serpentine soil. Adenostoma fasciculatum.

11. On highway 49, 200 yards south-east of collection site #10. Serpentine soil. Eremocarpus setigerus.

SCALE

MILES

KILOMETERS
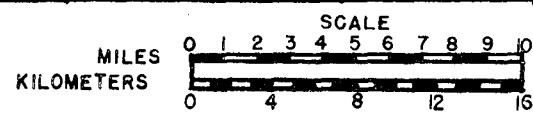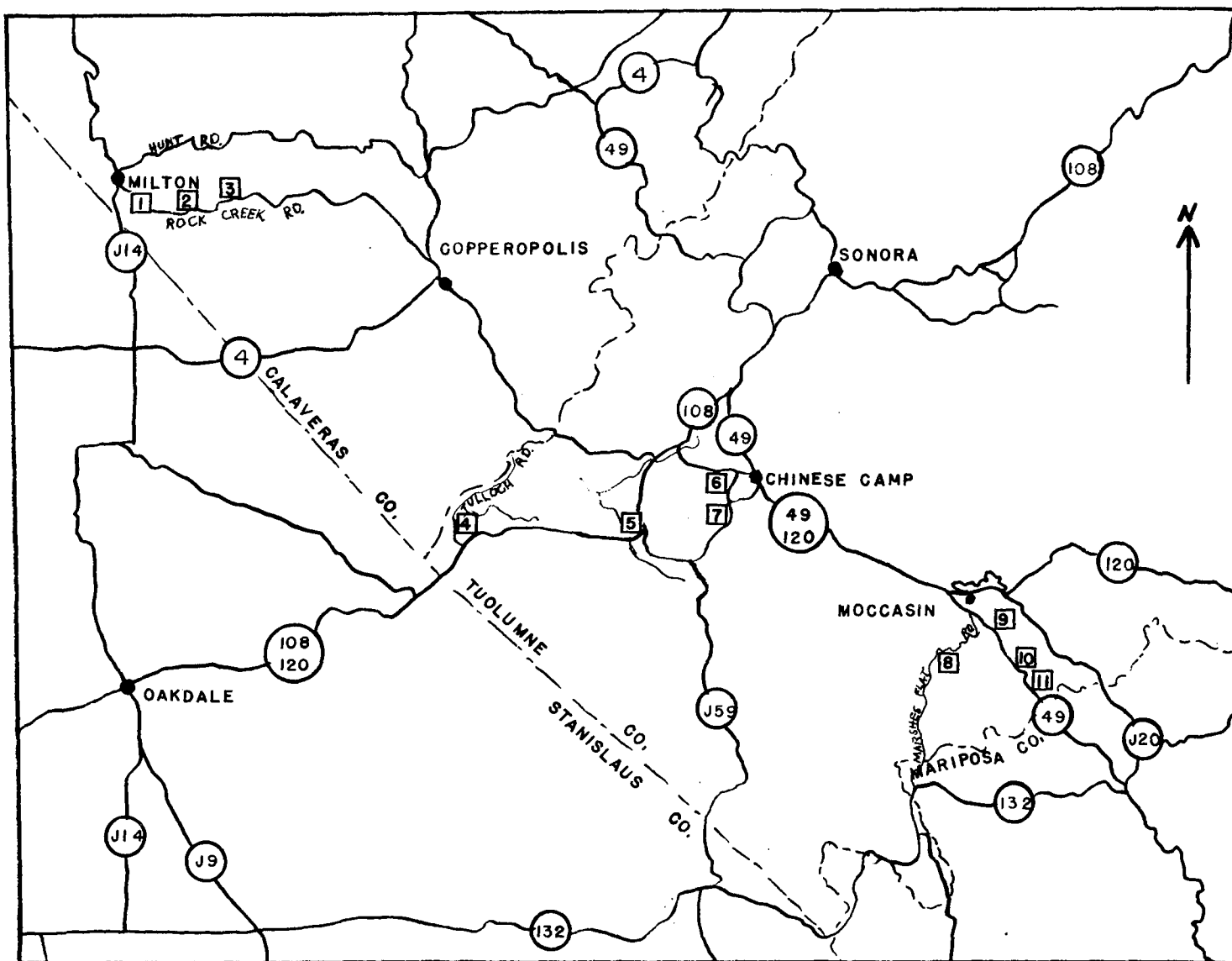
Figure 2.   Map of pond water collection site (ϕ).   Pond is on the north
            side of highway 124, 4.5 miles north-east of the junction of
            highways 104 and 124 at Ione.
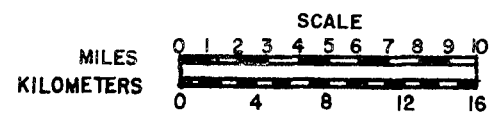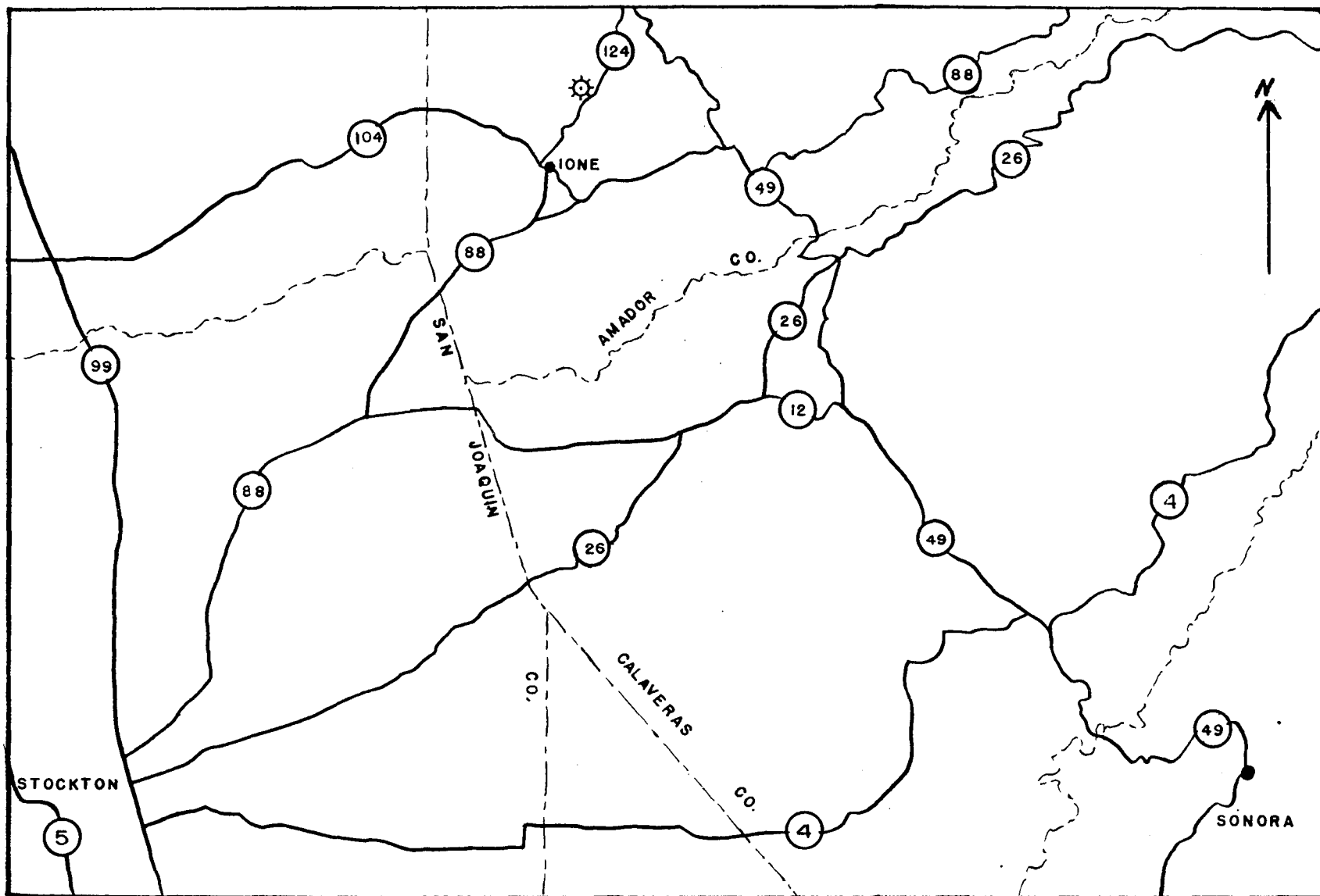
Calcium

Calcium levels in non-serpentine soils (except for the Pinus sabiniana location) ranged from 40 to 154 parts per million (ppm) and in serpentine soils from 42 to 138 ppm. Concentrations of calcium in non-serpentine plant tissues ranged from 99 to 384 ppm and in serpentine plants from 52 to 249 ppm. In all cases (except Pinus sabiniana, non-serpentine) the concentration of calcium was higher in plant tissues than in soil (Table II; Fig. 3).

Magnesium

Magnesium concentrations in non-serpentine soils ranged from non-detectable to 150 ppm and in serpentine soil from 2300 to 2900 ppm. Plant tissues from non-serpentine soils had magnesium concentrations of 20 to 130 ppm and in plants from serpentine soils, magnesium ranged from 40 to 210 ppm. In all but Adenostoma fasciculatum and Pinus sabiniana plant tissues had higher concentrations than the non-serpentine soil, and in all cases the reverse was true in serpentine soil (Table II; Fig. 4).

Sodium

Similar sodium concentrations were found in both non-serpentine (15 to 31 ppm) and serpentine (16 to 22 ppm). With one exception (Asclepias fascicularis), plant tissues had less sodium than the soil in which they grew and the values were relatively constant (2.4 to 8.2 ppm). Asclepias fascicularis from non-serpentine soil had 15.8 ppm and in serpentine soil 41.4 ppm (Table II; Fig. 5).

Potassium

Potassium concentrations in non-serpentine soils ranged from 16 to 51 ppm and from 13 to 20 ppm in serpentine soils. In all cases potassium concentrations in plant tissues were higher than in soil (69 to 785 ppm in non-serpentine soil; 34 to 708 ppm in serpentine soil). In general, potassium concentration in plants was highest in annuals and a herbaceous perennial (130 to 785 ppm), and lower in woody perennials (34 to 181 ppm) (Table II; Fig. 6).

Chromium

Chromium levels in non-serpentine soils were low (1.4 to 5.5 ppm) and only slightly higher in serpentine soils (7.9 to 38 ppm). No non-serpentine plant had detectable concentrations of chromium in the tissues and concentrations in the tissues of serpentine species were also low (non-detectable to 0.2 ppm) (Table II; Fig. 7).

Nickel

Nickel concentrations in non-serpentine soils were low (1.0 to 5.4 ppm) and higher in serpentine soils (41.0 to 82 ppm). No non-serpentine plant tissues had detectable concentrations of nickel and concentrations in the tissues of serpentine species were low (non-detectable to 0.6 ppm) (Table II; Fig. 8).

Calcium/Magnesium Ratios

The calcium/magnesium ratios in serpentine soils ranged from 0.02 to 0.12 and from 1.3 to 13.2 in those non-serpentine soils in which magnesium was at detectable levels. The calcium/magnesium ratio in plant tissue from serpentine areas ranged from 0.40 to 4.15 and in plants from non-serpentine locations ranged from 1.74 to 7.45. No plant tissues from serpentine soils had lower calcium/magnesium ratios

than the soils, while 3 of the 8 species from non-serpentine soils had
lower calcium/magnesium ratios than the soils (Table III).

Pond Water

The ion concentrations of pond water were: 16 ppm calcium;
35 ppm magnesium; 3.8 ppm sodium; 1.5 ppm potassium. Chromium and
nickel were non-detectable (Table IV).

Table I. Major roles of selected ions in plants.

Calcium: A constituent of the middle lamella, therefore may be
             important in "cementing" walls together; required as a
             cofactor by some enzymes involved in the hydrolysis of
             ATP and phospholipids (Noggle & Fritz, 1976); essential
             for normal membrane function (mechanism unknown);
             essential for absorption (Salisbury & Ross, 1978);
             plays an important role in amelioration of nickel,
             chromium and magnesium toxicity (Proctor & Woodell, 1975).

Magnesium: A constituent of the chlorophyll molecule; required non-
             specifically by a large number of enzymes involved in
             phosphate transfer (Noggle & Fritz, 1976); essential for
             full activity of the two principle CO_2-fixing enzymes;
             crucial to protein synthesis (Salisbury & Ross, 1978).

Sodium: Generally not considered essential for plant growth
             (Epstein, pers. comm.); usually removed by pumping
             mechanisms presumed to be similar to those of the sodium-
             pump in animal cells (Salisbury & Ross, 1978).

Potassium: Required as a cofactor for 40 or more enzymes; maintains
             electroneutrality in plant cells (Noggle & Fritz, 1976);
             important in stomate movements and maintenance of turgor
             (Salisbury & Ross, 1978).

Chromium: No evidence of any physiological function in plants; may
             be accumulated by some plants; may be a factor in some
             serpentine toxicity (Proctor & Woodell, 1975).

Nickel: May be accumulated by a few plants (Alyssum bertoloni),
             but no evidence for essentiality; common toxic element
             in serpentine soils (Proctor & Woodell, 1975).

DISCUSSION

Proctor & Woodell (1975) state that throughout the world serpentine vegetation is dominated by three growth forms; coniferous trees, sclerophyllous shrubs and grass-like plants and forbs. Consequently, I collected one conifer (Pinus sabiniana), two woody perennials (Adenostoma fasciculatum and Heteromeles arbutifolia), one herbaceous perennial (Asclepias fascicularis) and four herbaceous annuals (Clarkia biloba, Plantago hookeriana, Mimulus guttatus and Eremocarpus setigerus). This variety not only represented a "typical" serpentine assemblage of California native plants which also grow on non-serpentine soil but also meant that the tissue represented both annual growth into which ions might be moved rapidly and older tissues in which ions may be deposited or accumulated over a longer period of time.

The literature emphasizes the difficulty of determining whether or not any ion is actually available to plants (Proctor & Woodell, 1975). If an ion is capable of going into solution, it should be available for root uptake. To determine if there was any relationship between dissolved elements and those in the soils, I collected water for ion analysis. The pond near Ione was chosen because it was the only permanent body of standing water known to occur in a serpentine location relatively close to the plant collection sites.

Replicate samples of the dried material were not used, therefore, the resultant data constitutes a single value for each species. Soil and water samples were treated in the same way resulting in a single value for the sample. This method of data collection un-

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fortunately prevents statistical treatment of the data. Because there was no data in the literature on ion concentrations of California native non-serpentine plants, and only one study in which there was some analysis of ion concentrations in the same species on serpentine and non-serpentine soils (White, 1971), this study was designed as a preliminary survey. To analyze six ions in eight species on serpentine and non-serpentine soil required a total of ninety-six plant tissue analyses. There were eleven different soil collection locations and three analyses of each was done for each of the six ions for a total of one hundred and ninety-eight soil analyses. The single water analysis added six more for a total of three hundred separate ion analyses. To perform sufficient replicates on each of these analyses to be "statistically significant" would involve a large amount of time. However, for further study of a single species, replicates for statistical analysis should be performed.

Most of the ions selected for this study (Table I) were those most frequently measured in serpentine soils. The imbalance of calcium and magnesium is most commonly thought to be the reason for serpentine infertility. Chromium and nickel are two of the most common toxic elements in serpentine soil. Potassium has several essential roles in normal plant growth. Although sodium is not normally essential for plant growth it is the single most important cation in animal cells, and was included out of curiosity.

Calcium:

Soil content of any ion depends on geological origin. Calcium concentrations of serpentine soils may range from non-detectable to 6000 ppm (Proctor & Woodell, 1975). Serpentine soils are generally

considered to be deficient in calcium, but Jones et al., (1976) make the important point that this is true of some but not all serpentine soils. Jones' generalization applies to the soils tested, in which there was considerable variation in calcium content. [All but two of the serpentine soils had calcium concentrations below the "usual range" of 80 to 1600 ppm for serpentine soil (Proctor & Woodell, 1975)]. The lowest calcium level occurred in one of the non-serpentine soils, six of the serpentine soils had calcium levels in the range of 40 to 50 ppm, four of the non-serpentine soils had calcium concentrations below 80 ppm, and the highest serpentine value of 138 ppm was in the range (124 to 154 ppm) of three of the non-serpentine soils. The high calcium concentration (458 ppm) in the _Pinus sabiniana_ non-serpentine soil may indicate that the soil in this location is derived from a calcareous vein (Table II; Fig. 3).

Proctor & Woodell (1975: 330) point out that "the calcium requirements of plants are much lower than was thought". Tobacco, maize and a variety of other crops and pasture plants have been successfully grown in media with 2 ppm calcium or less when other ions are in balanced supply. If the value of 16 ppm calcium in the pond water represents an approximation for calcium availability, then these serpentine soils are not "deficient" in calcium assuming no interference from other elements. The species collected for the study may owe part of their ability to grow in both serpentine and non-serpentine soils to their ability to use the available calcium to ameliorate the toxic effects of other ions such as nickel, chromium and excess magnesium (Proctor & Woodell, 1975; Marrs & Proctor, 1976).

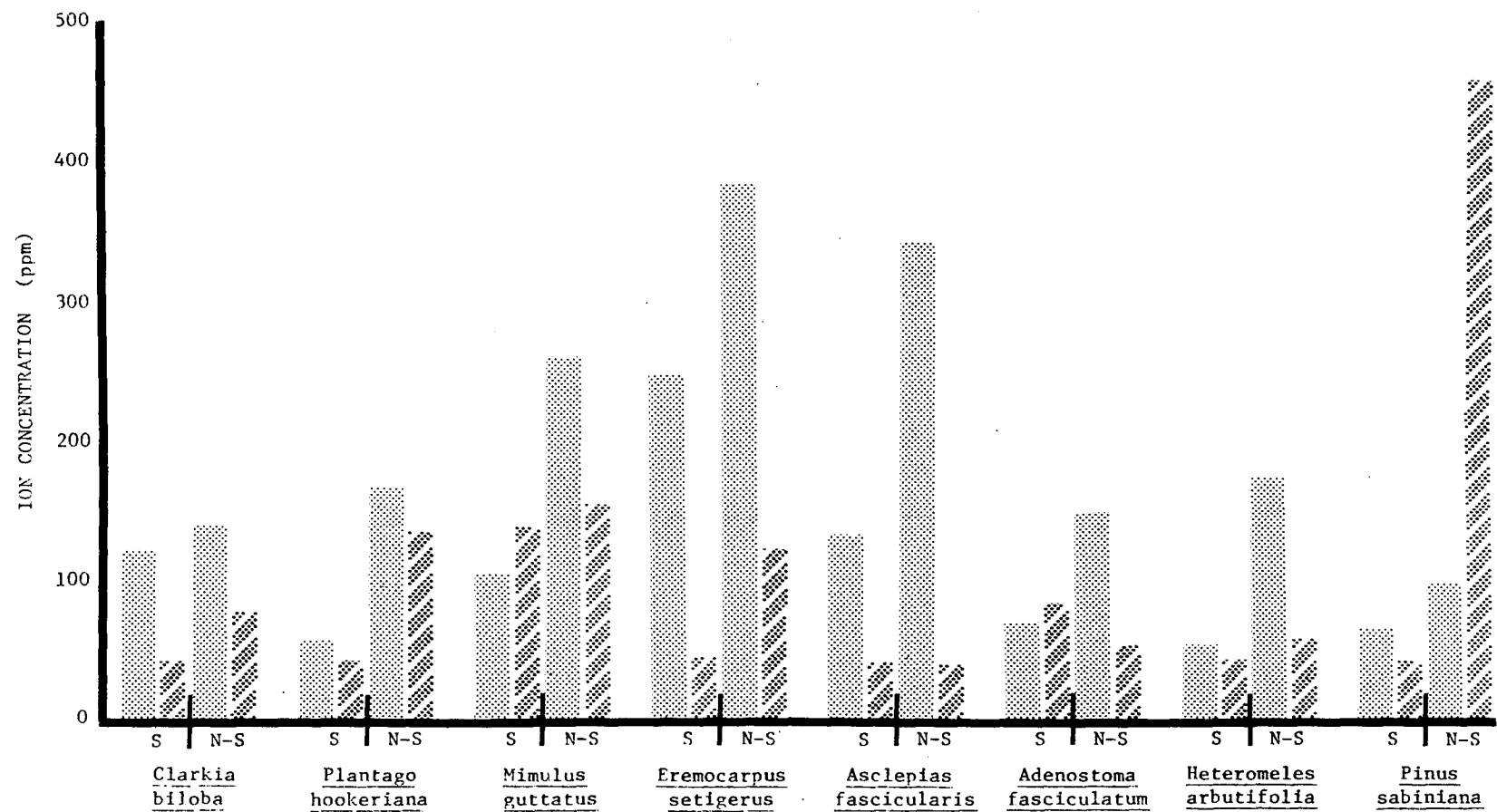All but one non-serpentine plant had plant/soil calcium

Figure 3. Calcium ion concentrations in plant tissues (▒▒▒▒) excluding roots and soil
(░░░░) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

ratios above 1.0 (1.27 to 8.55) as did all but two of the serpentine soil plants (1.33 to 5.41) (Table V) indicating the plant's ability to accumulate calcium from the soil. The two serpentine soil species which had plant/soil ratios less than 1.0 were from the highest calcium-content serpentine soils (Table I). In Mimulus guttatus (serpentine) tissue calcium was 105 ppm and soil calcium was 138 ppm. The non-serpentine soil from which the same species was collected had only slightly higher calcium (154 ppm), but tissue calcium was two and a half times higher (259 ppm). A similar situation was found in Adenostoma fasciculatum, but in this case the non-serpentine had less calcium than the serpentine soil (86 ppm serpentine; 52 ppm non-serpentine). The most reasonable explanation is that this illustrates the problem of high levels of magnesium interfering with calcium uptake. Such a situation might be expected to occur in non-endemic plants living in serpentine areas, because non-serpentine plants are less capable of selectively absorbing calcium and restraining magnesium uptake (Proctor & Woodell, 1975). The low plant/soil calcium ratio in Pinus sabiniana from non-serpentine soil is most likely only a reflection of the high soil calcium rather than impairment of calcium uptake.

Magnesium:

All serpentine soils are characterized by high magnesium levels, and the soils tested were no exception with concentrations ranging from 2300 to 2900 ppm. In serpentine soils from Napa, California, magnesium levels as high as 6000 ppm and as low as 800 ppm have been reported (Proctor & Woodell, 1975), so the values found here are intermediate. Although serpentine soil magnesium concentrations are high, the actual concentration available to the plant may be considerably

lower. (Table II; Fig. 4). The value of 35 ppm in pond water represents magnesium in solution in standing water in a serpentine area (Table IV). The relative concentration of ions at the soil-root interface available to the plant may be considerably larger (Main, 1974; Jones, et al., 1976; Wallace, et al., 1977; Willett & Batey, 1977). In contrast, the non-serpentine soils had magnesium concentrations ranging from non-detectable to 150 ppm.

Magnesium is essential for plant growth because it is a constituent of the chlorophyll molecule, essential for maximum rates of most and perhaps all of the hundreds of enzymatic reactions involving ATP. In addition it enhances the activity of other respiratory enzymes and is essential for full activity of the two principle carbon dioxide fixing enzymes, and is crucial for protein synthesis (Salisbury & Ross, 1978). Considering the essentiality of this element, it is not unusual that it was present in the tissue of plants collected from soil in which the concentration was less than 0.1 ppm.

In all cases plants from serpentine areas had less magnesium in the tissue than in the soil in which they were growing (Plant/soil magnesium ratios of 0.01 to 0.087) (Table V), indicating the ability of these plants to exclude this element when it is present in excess concentration in the soil. In contrast, in all but two cases plants from non-serpentine areas had higher magnesium concentrations than the soil in which they were growing (plant/soil magnesium ratios of 1.4 to 13 and above) (Table V), illustrating the reverse phenomenon of accumulation of the element from low magnesium soil. It is noteworthy that the same species are capable of exclusion or accumulation depending upon the growing medium, and this may help to explain the success of the species

examined in inhabiting both serpentine and non-serpentine soils.

Pinus sabiniana was one of the exceptions to the generalization that non-serpentine plants accumulated magnesium. Tissue magnesium was identical and comparatively low (40 ppm) in plants from both soil types. However, this non-serpentine soil had the highest magnesium content of any non-serpentine soil analyzed, and the soil megnesium value of 150 ppm was higher than all but two of the serpentine plant tissues. Pinus sabiniana may simply be maintaining a "normal" tissue magnesium in any soil. It would be worth further investigation to determine if this is one of the mechanisms by which this species is able to tolerate a wide range of soil types. The other exception (Adenostoma fasciculatum, non-serpentine) had the lowest tissue magnesium of any plant analyzed. It is possible that the magnesium requirement of this species is low.

Despite the essentiality of magnesium, high concentrations are toxic. Some non-endemic plants evidently engage in "luxury consumption" of magnesium when growing in serpentine soils (Marrs & Proctor, 1976). Elevated magnesium levels depress development of primary phloem and other aspects of growth. As little as 1 ppm can decrease root growth in some non-serpentine species. However, many plants, both serpentine endemics (serpentine plants) and non-endemics can tolerate increased soil magnesium, and this tolerance has been shown to be genetic (Main, 1974; Proctor & Woodell, 1975).

It has long been recognized that the interaction between calcium and magnesium is important in serpentine soil. In the early 1900's it was suggested that a calcium/magnesium ratio above 1.0 was necessary for healthy plant growth, but the large amount of species

variation makes it impossible to apply a single standard to all plants. Magnesium toxicity depends on calcium concentration because increased magnesium tends to inhibit absorption of calcium (Proctor & Woodell, 1975).

Many serpentine plants contain more magnesium than calcium, but calcium absorption is "more avid" in serpentine soils. There are few data for non-serpentine plants living on serpentine soil, but it appears that they are less able to restrict magnesium uptake and selectively absorb calcium (Proctor & Woodell, 1975). As usual, there are exceptions to such generalizations. Four of the species from serpentine soil examined in this study showed higher magensium than calcium in the tissues (Plantago hookeriana, Mimulus guttatus, Asclepias fascicularis and Heteromeles arbutifolia), two species had essentially equal concentrations of the two elements (Clarkia biloba and Adenostoma fasciculatum), while two had higher tissue calcium than magnesium (Eremocarpus setigerus and Pinus sabiniana)(Table II). The difference between calcium and magnesium in Pinus sabiniana (64 ppm calcium, 40 ppm magnesium) is not large, but tissue calcium in Eremocarpus setigerus was 259 ppm while magnesium was only 60 ppm. Eremocarpus setigerus is evidently able to absorb calcium with considerable "avidity".

Another way to compare calcium and magnesium is to consider the ratios of these elements in plant tissues of the same species growing in serpentine and non-serpentine soils (Table VI). When the tissue calcium ratio between plants from the two soil types is closer to unity (tissue concentration of calcium similar in plants from serpentine and non-serpentine areas), the tissue magnesium ratio between serpentine and non-serpentine is also closer to unity (less
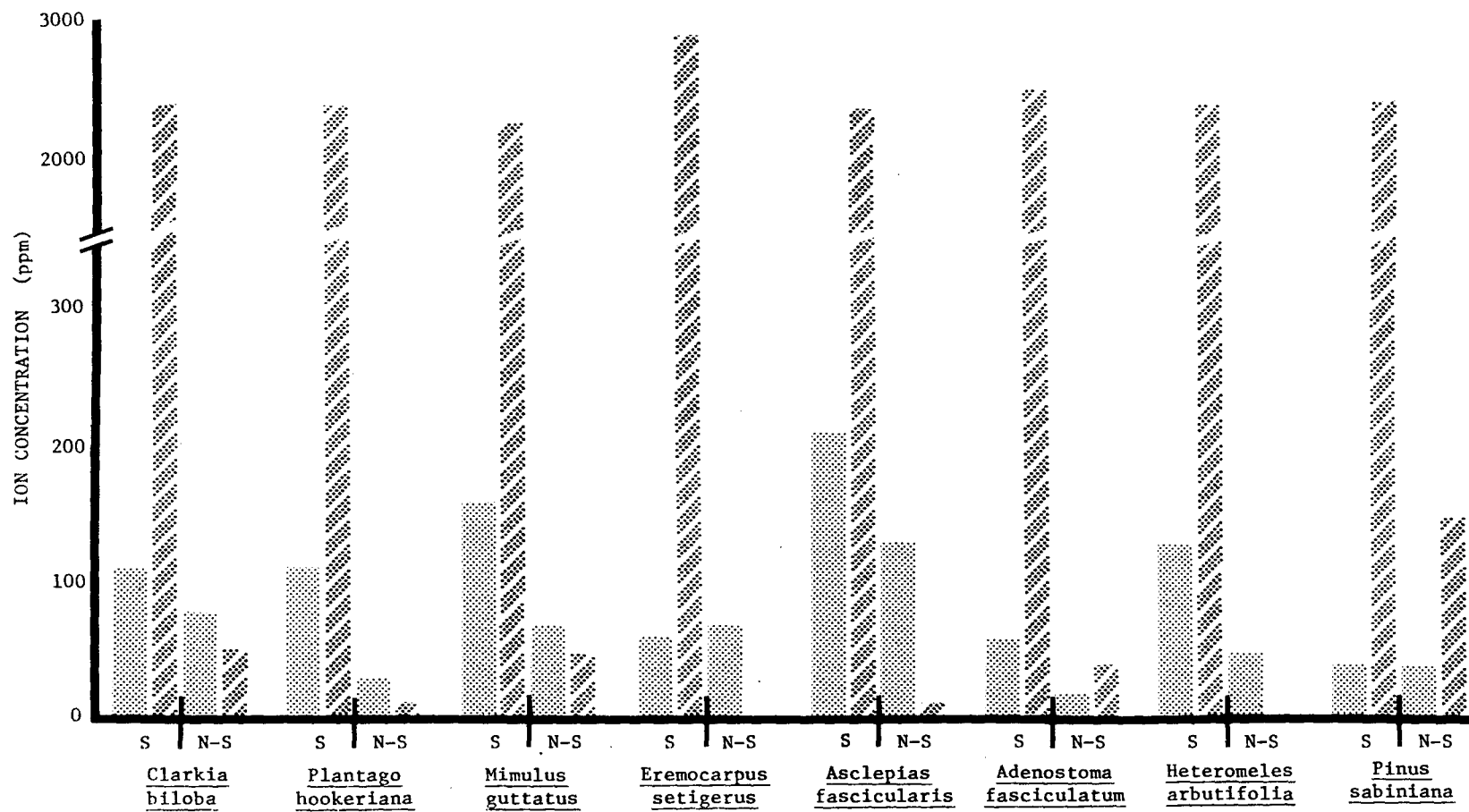
Figure 4. Magnesium ion concentrations in plant tissues (▒▒▒) excluding roots and soil (▒▒▒) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

difference in tissue magnesium between plants from serpentine and non-serpentine soils). Three species (Clarkia biloba, Eremocarpus setigerus and Pinus sabiniana) illustrate this phenomenon. It may indicate their ability to restrict magnesium uptake while selectively absorbing calcium in serpentine soil. In all other species the difference in tissue calcium between the soils is large (ratio above 2.0) and the difference in tissue magnesium is also large (ratio 0.6 or less), possibly showing the inability of these species to selectively restrict magnesium uptake and increase calcium uptake. It would be interesting to examine this relationship in greater detail.

That the relationship between calcium and magnesium is not yet completely understood is best expressed by the final paragraph of Proctor & Woodell's (1975) discussion of calcium/magnesium interactions.

"The precise way in which calcium and magnesium interact during uptake is not yet clear. Is there both competitive and non-competitive inhibition as Grover and Madhok have suggested? How do magnesium and calcium interact inside the cell? What is the biological mechanism of magnesium toxicity, and of the universal ability of calcium to ameliorate toxicity, not only of magnesium but of other ions?" (Proctor & Woodell, 1975: 336).

Sodium:

The concentration of sodium in serpentine soils ranged from 16 to 22 ppm, and in non-serpentine soils from 15 to 31 ppm. Although these two soil types were derived from different rock sources, the sodium concentrations in all but two cases did not differ much between the serpentine and non-serpentine soils. The exceptions were the non-serpentine soils in which Mimulus guttatus and Eremocarpus setigerus were collected with sodium concentrations up to twice that of other soils (Table II; Fig. 5).

In all but one plant (Asclepias fascicularis, serpentine) sodium concentrations were lower than in the soil in which the plant

grew, and showed little variation between species or between the same species from different soil. The plant/soil sodium ratio (Table V) illustrates whether the plant is excluding sodium (ratio less than 1.0) or accumulating sodium (ratio greater than 1.0). For example, sodium concentration in _Mimulus guttatus_ on non-serpentine soil (plant 8.2 ppm, soil 31 ppm) is higher than the same species in serpentine soil (plant 5.6 ppm, soil 16 ppm). However, the plant/soil sodium ratio of the serpentine plant is 0.35 and that of the non-serpentine plant is 0.26. The lower value of this ratio for the non-serpentine plant indicates increased ability of this plant to exclude sodium.

Sodium ions are apparently excluded from plants by a pumping mechanism presumed to be similar to that of animal cells. A pump in the cell membrane removes sodium that diffuses in (as in animal cells) and a pump in the vacuolar membrane apparently transports some of the cytoplasmic sodium into the vacuole. In the roots of most species much of the sodium in the vacuoles is never transported to the shoots, thus excluding sodium from the aerial tissues (Salisbury & Ross, 1978).

Asclepias fascicularis was unusual. Plants collected on non-serpentine soil had plant/soil sodium ratio of 0.94, indicating that sodium concentrations were almost the same in the plant as in the soil. Plants from the serpentine soil had a plant/soil sodium ratio of 2.56 indicating plant tissue sodium concentrations of two and a half times higher than in the soil. Although sodium is generally not considered essential for plants, there may be some exceptions, and this species is worth further investigation as a possible sodium-dependent species (Epstein, pers. comm.).
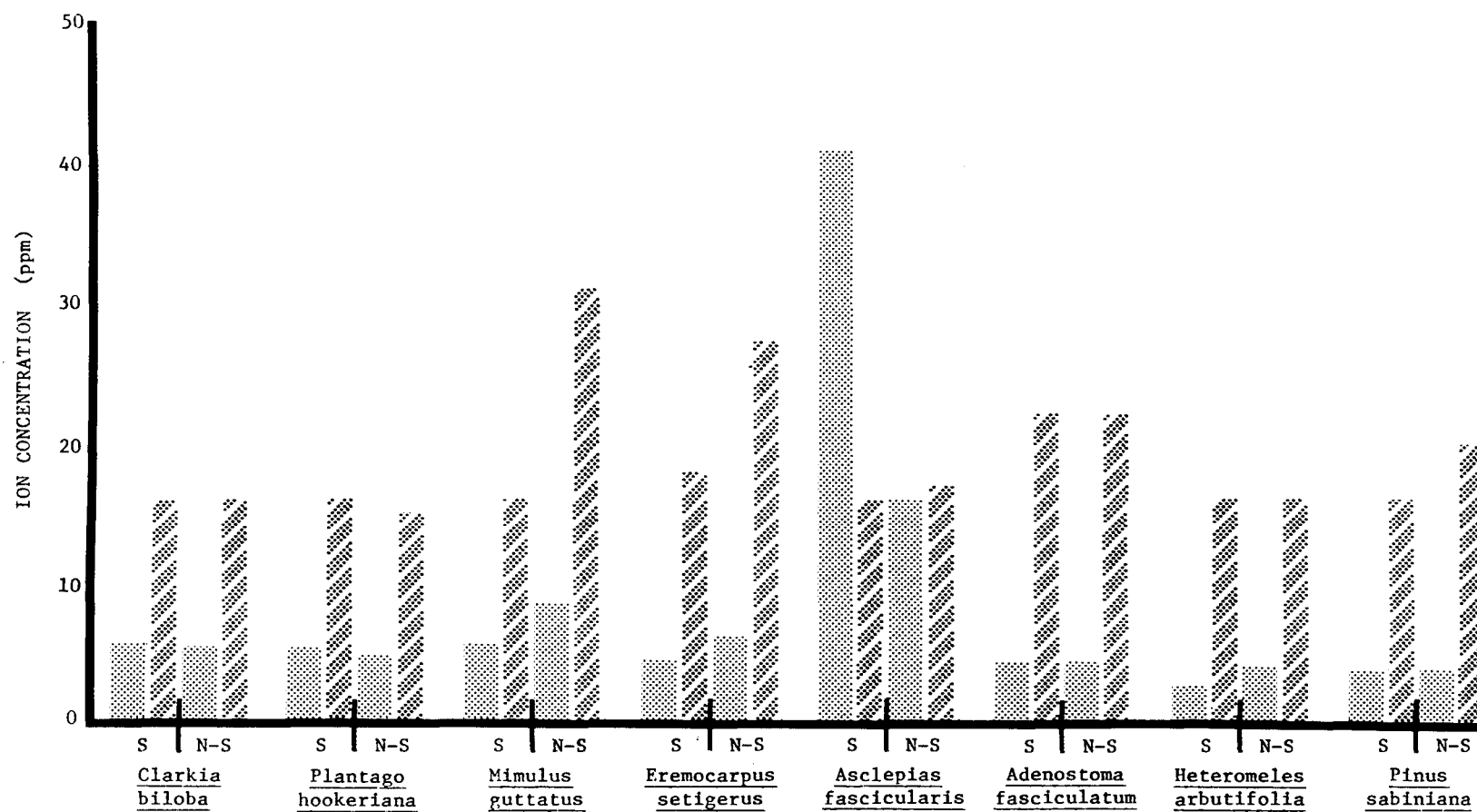
Figure 5. Sodium ion concentrations in plant tissues (░░░░) excluding roots and soil (▒▒▒▒) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

Potassium:

Potassium is an essential element for normal plant growth. It activates a variety of enzymes involved in glycolysis and starch synthesis, is involved in translocation of ions, charge balancing of anions and maintenance of turgor (Salisbury & Ross, 1978).

Soil potassium levels were higher in non-serpentine than serpentine, but in most cases the differences were not large (Table II; Fig. 6). The range for serpentine soils was 13 to 20 ppm and for non-serpentine 16 to 51 ppm.

All plants had higher potassium concentrations than the soil in which they were growing. In all but two species, plants from non-serpentine soil had higher concentrations of potassium than the same species from serpentine soil. In most species this difference was negligible, but son-serpentine Adenostoma fasciculatum had twice the potassium of the same species on serpentine soil and non-serpentine Asclepias fascicularis had almost three times the potassium concentration of the same species from serpentine soil. The condition found in these two species may represent extreme examples of that found in the other species; that is plants growing under the more stressful conditions of serpentine soil have difficulty in accumulating some ions. The most notable plant in regard to potassium was Eremocarpus setigerus. In this case the serpentine plants had almost three times as much potassium (481 ppm) as the non-serpentine plants (181 ppm). There was no obvious morphological difference between plants from the two soil types. I have no idea why potassium is apparently accumulated to such an extent in this plant in serpentine soil and can only suggest that this poses an interesting question for further study.
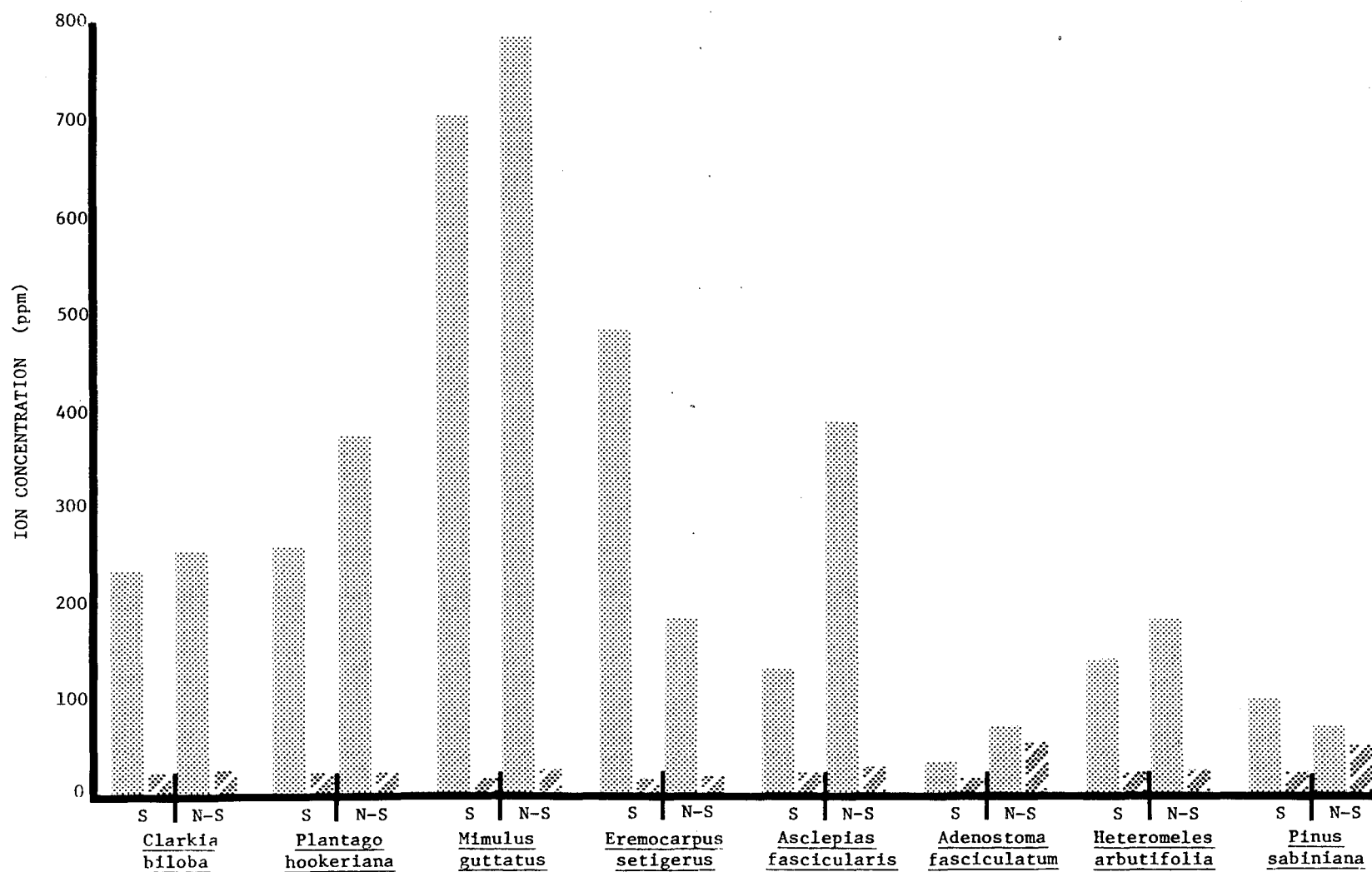
Figure 6. Potassium ion concentrations in plant tissues (▒▒▒▒) excluding roots and soil (▒▒▒▒) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

The most obvious difference in potassium content between species was between annual and perennial tissues. The annual plants had high potassium concentrations (181 to 785 ppm), the herbaceous perennial was also high (130 to 386 ppm), while the perennial tissues were relatively low (34 to 181 ppm). This is almost as expected considering the role of potassium in actively growing plant tissue (Table I). The tissues of annual plants are actively involved in the processes which require potassium, while older tissue contains a higher percentage of dead cells. The woody tissues of perennials also provide support, while annual plants depend largely upon turgor for leaf and stem rigidity.

Chromium:

In all non-serpentine soils the concentration of chromium was 5.5 ppm or less. Five of the serpentine soils had only slightly higher values (7.9 ppm), but three of the serpentine soils had concentrations above 30 ppm (Table II; Fig. 7). There is no specific concentration of chromium that is considered "toxic" because of the complex interactions between ions. Some reported values of chromium in serpentine soils are much higher than those reported in this study, with concentrations varying from 5 to 1000 ppm total chromium in normal soils. Serpentine soils frequently have total chromium contents which are very much higher than these, up to over 100,000 ppm (Proctor & Woodel, 1975). It is possible that chromium is not in high enough concentrations in these soils to be a major toxic element for the species examined.

No plants collected from non-serpentine soils had any detectable chromium in the tissues. These species are evidently able
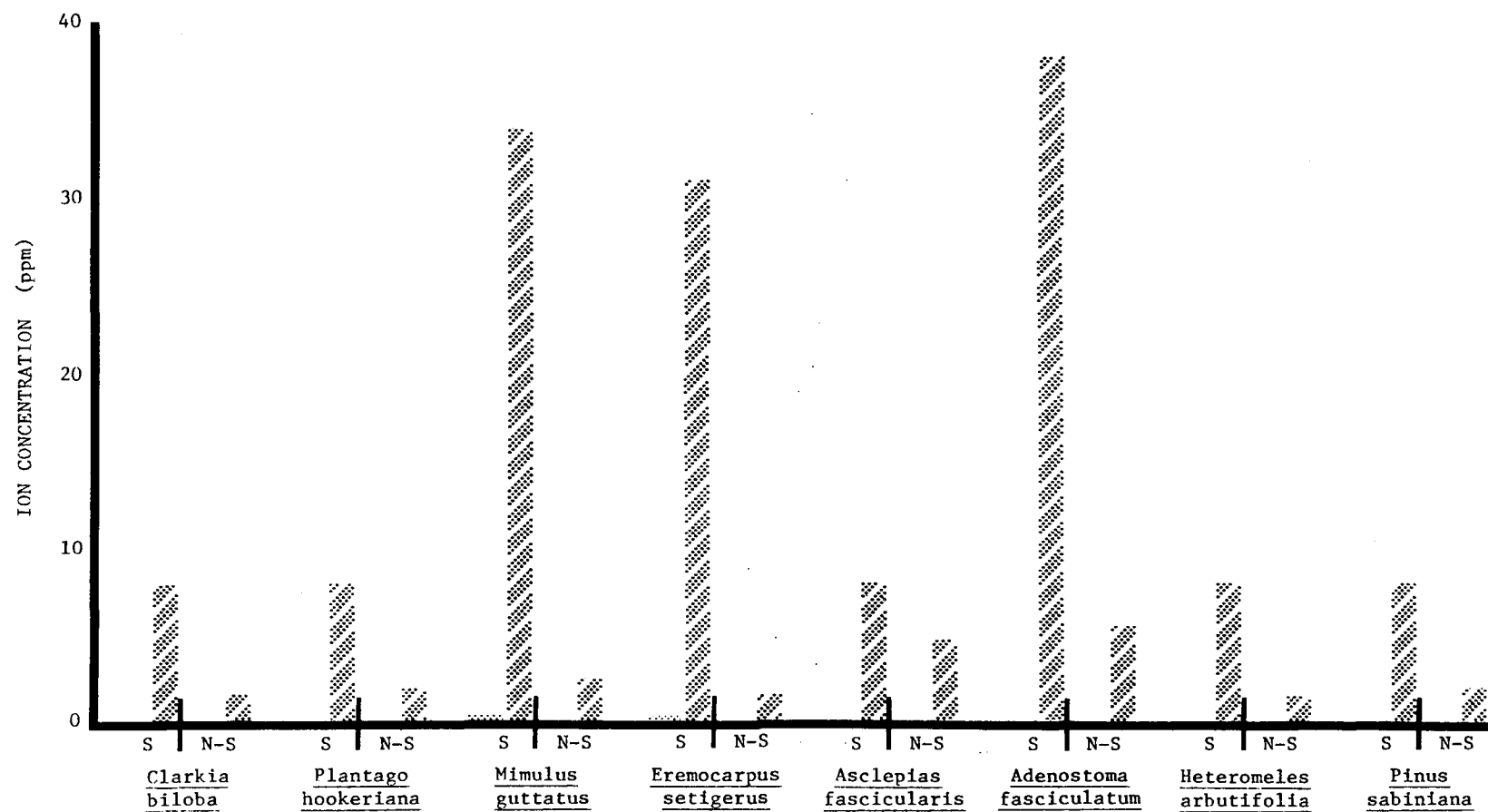
Figure 7. Chromium ion concentrations in plant tissues (▒▒▒) excluding roots and soil
(░░░) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

to exclude chromium at the low levels present in the soil in which they are growing.

Only two of the plants collected in serpentine areas (Mimulus guttatus and Eremocarpus setigerus) had detectable levels of chromium (0.12, 0.17 ppm) in the tissues. Both species grew on soils with chromium levels above 30 ppm. The presence of low chromium in the tissues in the presence of much higher levels in the soil may indicate the ability of these species to effectively exclude almost all soil chromium while tolerating a small amount in the tissues. Such a tolerance has been indicated by Pratt (1966, in Proctor & Woodell, 1975). Pratt, working mainly with cultivated plants, collected data which showed that on non-serpentine soils a chromium content less than 2 ppm dry matter in the above ground parts is usual. Other native plants growing on non-serpentine soil had a tissue chromium content of 4 to 120 ppm. However, on serpentine soils plants usually, but not always, contain much higher quantities of chromium (Proctor & Woodell, 1975; Shewry & Peterson, 1976).

It is worth noting that Adenostoma fasciculatum, collected from a soil with the highest chromium level found (38 ppm) had no detectable chromium in the tissue. Evidently this species can effectively exclude chromium even in the presence of elevated soil concentrations. Some true serpentine endemics are capable of excluding chromium at very high soil levels (125,000 ppm) while others can tolerate high tissue chromium (48,000 ppm in leaves) (Lyon, et al., 1970; Proctor & Woodell, 1975).

Nickel:

Several methods have been used to measure nickel content in

soil. Unfortunately the same soil treated by different methods may give
different values for this ion. There is apparently no method which will
reliably measure nickel availability to the plant. According to Proctor
(1972, cited in Proctor & Woodell, 1975) "plant available" nickel is
difficult to assess because the more labile forms of nickel are in
different forms in different soils.

Using the aqua regia extraction method, the nickel concentra-
tions in non-serpentine soils were low (5.4 ppm or less) compared to
that of serpentine soil (41 to 82 ppm). However, these serpentine
values are low compared with other serpentine soils in which nickel
concentrations can reach several thousand ppm, and only slightly above
the average of 30-40 ppm nickel for non-serpentine soils (Proctor &
Woodell, 1975).

No plants collected in non-serpentine areas had any
detectable nickel in the tissues indicating the ability to completely
exclude this ion when soil concentrations are low. Two species from
serpentine soil (Asclepias fascicularis and Pinus sabiniana) also had
no detectable tissue nickel at soil concentrations of 82 ppm. The
remaining six species from serpentine soil had low nickel (less than
1.0 ppm), again indicating the ability to exclude most of this
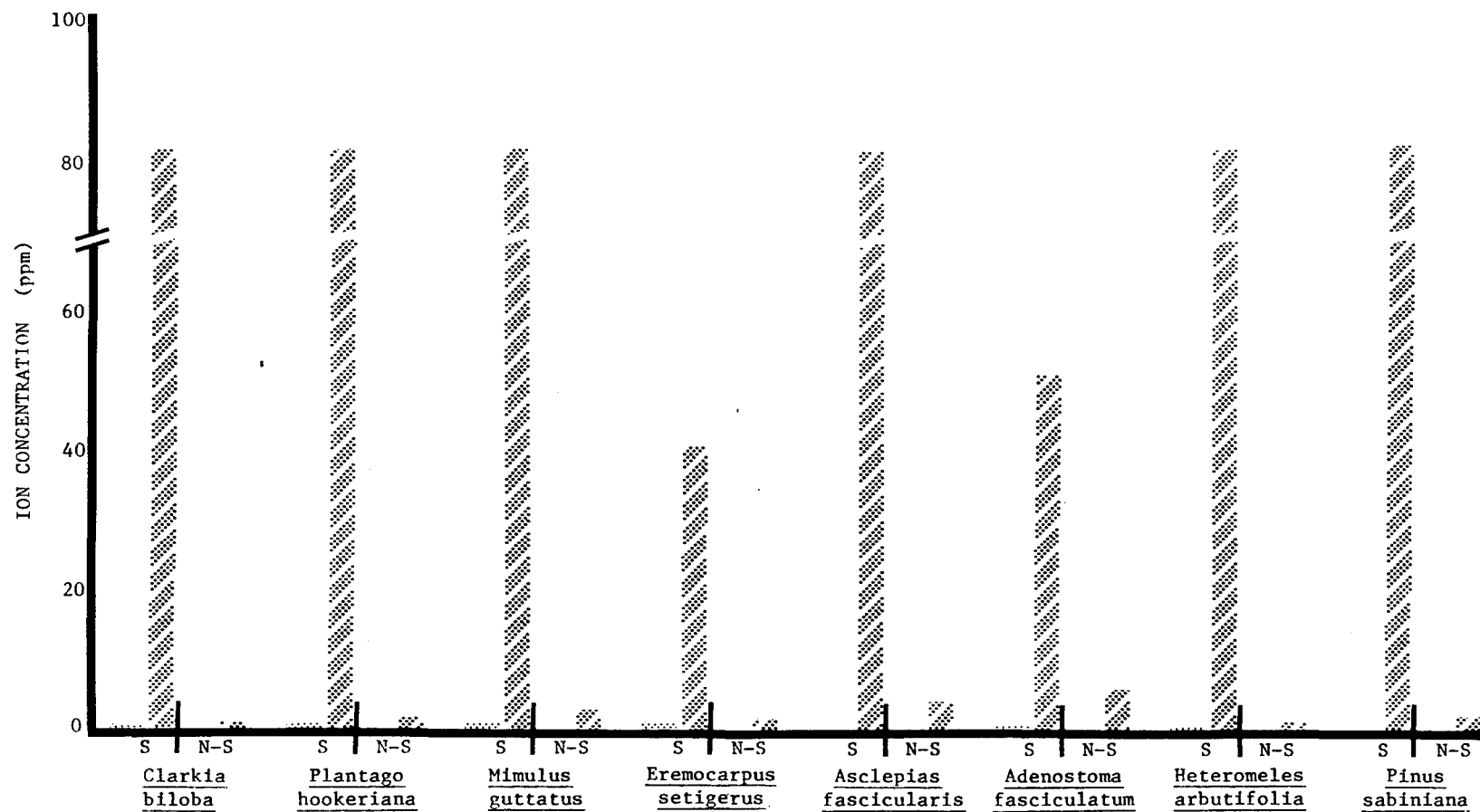potentially toxic element (Table II; Fig. 8).

Figure 8. Nickel ion concentrations in plant tissues (▓▓▓) excluding roots and soil (▒▒▒) in which the plant was growing in serpentine (S) and non-serpentine (N-S) soil.

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SUMMARY

Eight species of California native plants (Clarkia biloba,

Plantago hookeriana, Mimulus guttatus, Eremocarpus setigerus, Asclepias

fascicularis, Adenostoma fasciculatum, Heteromeles arbutifolis and

Pinus sabiniana) and samples of the soil in which they were growing

were collected from serpentine and non-serpentine areas. The con-

centration of selected ions (calcium, magnesium, sodium, potassium,

chromium and nickel) in the aerial plant parts and in the soil were

determined by atomic absorption. The same ions were also measured in

a sample of pond water from a serpentine area.

In general, serpentine soil had less calcium and more

magnesium, chromium and nickel than non-serpentine soil. Sodium and

potassium content in the two soil types were similar. The calcium/

magnesium ratio of serpentine soil was 0.12 or less and 1.3 or higher

in non-serpentine soil.

In general, plants growing in serpentine soil accumulated

less calcium and potassium and more magnesium than the same species

growing in non-serpentine soil. Sodium concentrations were similar

between the same species from the two soil types. No non-serpentine

plants had any detectable level of tissue chromium or nickel, these

ions appearing only in the tissues of some plants growing in serpentine

soil.

Some exceptions to these generalizations or variations from

the condition in other species examined suggest possible questions for

further work. The most notable are:

1. Despite a soil calcium/magnesium ratio of 0.02, Eremocarpus

setigerus had less tissue magnesium in serpentine than in
non-serpentine soil suggesting an efficient mechanism for
exclusion of this potentially toxic element.

2. When the tissue calcium ratio between non-serpentine and
   serpentine of a species is close to 1.0, the tissue magnesium
   ratio between non-serpentine and serpentine of the same
   species is also close to 1.0. This was found in three
   species (Clarkia biloba, Eremocarpus setigerus and Pinus
   sabiniana) and may indicate that increased ability to restrict
   magnesium is linked to increased ability to absorb calcium.

3. Asclepias fascicularis from non-serpentine had twice the
   sodium content of any other non-serpentine species examined,
   and from serpentine soil had seven times the sodium content
   of any other serpentine species. Although few plants require
   sodium, it would be interesting to determine whether or not
   this species of Asclepias is sodium-dependent.

4. Is there usually more potassium in annual plant tissue than
   in second year and older leaves and stems?

5. Why is the tissue potassium of Mimulus guttatus almost twice
   that of any other species examined?

6. Why is tissue potassium of Eremocarpus setigerus more than
   two and a half times higher when growing in serpentine than
   in non-serpentine when most other species examined had less
   tissue potassium when growing in serpentine soil?

That this brief survey has disclosed so many possible

avenues for further research is one reason why the study of serpentine

areas "excites the analytical mind" (Kruckeberg, 1969 in Proctor &

Woodell, 1975: 265).

Table II. Ion concentrations (ppm/g dry weight) in plant tissues (P) soil (S).

Species / Soil type	Calcium		Magnesium		Sodium		Potassium		Chromium		Nickel	
	P	S	P	S*	P	S	P	S	P	S	P	S
Clarkia biloba												
Serpentine	119	42	110	2400	5.6	16	234	20	⊖	7.9	0.35	82
Non-serpentine	139	76	80	50	5.2	16	256	23	⊖	1.5	⊖	0.9
Plantago hookeriana												
Serpentine	56	42	110	2400	5.2	16	258	20	⊖	7.9	0.46	82
Non-serpentine	167	132	30	10	4.8	15	370	21	⊖	1.8	⊖	1.4
Mimulus guttatus												
Serpentine	105	138	160	2300	5.6	16	708	16	0.17	34	0.58	82
Non-serpentine	259	154	70	50	8.2	31	785	26	⊖	2.4	⊖	2.9
Eremocarpus setigerus												
Serpentine	249	46	60	2900	4.6	18	481	13	0.12	31	0.44	41
Non-serpentine	384	124	70	⊖	6.0	27	181	16	⊖	1.5	⊖	1.2
Asclepias fascicularis												
Serpentine	131	42	210	2400	41	16	130	20	⊖	7.9	⊖	82
Non-serpentine	342	40	130	10	16	17	386	27	⊖	4.6	⊖	3.6
Adenostoma fasciculatum												
Serpentine	70	86	60	2500	4.2	22	34	15	⊖	38	0.18	51
Non-serpentine	149	52	20	40	4.2	22	69	51	⊖	5.5	⊖	5.4
Heteromeles arbutifolia												
Serpentine	52	42	130	2400	2.4	16	138	20	⊖	7.9	0.17	82
Non-serpentine	173	58	50	⊖	4.0	16	181	21	⊖	1.4	⊖	1.0
Pinus sabiniana												
Serpentine	64	42	40	2400	3.6	16	95	20	⊖	7.9	⊖	82
Non-serpentine	99	458	40	150	3.8	20	69	50	⊖	1.9	⊖	1.9

* Magnesium content of serpentine soil ± 50 ppm.

⊖ Concentration of ion below reliable detection limit of the instrument (about 0.1 ppm).

Table III. Calcium/magnesium ratios in plant tissues and soils.
(S = serpentine; NS = non-serpentine).

Species	PLANT TISSUE		SOIL	
	S	NS	S	NS
Clarkia biloba	1.08	1.74	0.12	1.52
Plantago hookeriana	0.51	5.57	0.02	13.20
Mimulus guttatus	0.66	3.70	0.06	3.08
Eremocarpus setigerus	4.15	5.49	0.02	-0-
Asclepias fascicularis	0.62	2.63	0.02	4.00
Adenostoma fasciculatum	1.67	7.45	0.03	1.30
Heteromeles arbutifolia	0.40	3.46	0.02	-0-
Pinus sabiniana	1.60	2.48	0.02	3.05

-0- No detectable Mg in the non-serpentine soil sample.

Table IV. Ion concentrations (ppm) in serpentine area pond water
(location shown in Fig. 2).

Ion	Concentration ppm
Calcium	16
Magnesium	35
Sodium	3.8
Potassium	1.5
Chromium	-0-
Nickel	-0-

Ca/Mg ratio: 0.46

-0- = Concentration of ion below reliable detection limit of the
instrument (about 0.1 ppm).

Table V. Plant/soil ratios of calcium, magnesium and sodium   (S = serpentine; NS = non-serpentine).

Species	Calcium		Magnesium		Sodium	
	S	NS	S	NS	S	NS
Clarkia biloba	2.83	1.83	0.045	1.6	0.35	0.33
Plantago hookeriana	1.33	1.27	0.045	3.0	0.33	0.32
Mimulus guttatus	0.76	1.68	0.069	1.4	0.35	0.26
Eremocarpus setigerus	5.41	3.10	0.021	-0-	0.26	0.22
Asclepias fascicularis	3.12	8.55	0.087	13.0	2.56	0.94
Adenostoma fasciculatum	0.81	2.87	0.024	0.5	0.19	0.19
Heteromeles arbutifolia	1.24	2.98	0.054	-0-	0.15	0.25
Pinus sabiniana	1.52	0.22	0.017	0.267	0.23	0.19

-0- = No detectable Mg in non-serpentine soil.

Table VI. NS/S = Non-serpentine/serpentine ratios in calcium and
           magnesium.

Species	NS/S Tissue Ca	NS/S Tissue Mg
Clarkia biloba	1.2	0.72
Plantago hookeriana	3.0	0.27
Mimulus guttatus	2.5	0.44
Eremocarpus setigerus	1.5	1.17
Asclepias fascicularis	2.6	0.62
Adenostoma fasciculatum	2.1	0.33
Heteromeles arbutifolia	3.3	0.38
Pinus sabiniana	1.5	1.0

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APPENDIX

Plant Species Studied

1. __Clarkia biloba__ (Durand) Nels. & Macbr. (Onagraceae). Erect Annual:
2-10 dm. tall, simple or branched above; buds pendulous; fl-
tube 1-4 mm. long, with hair-ring near summit; sepals 6-17 mm.
long, united and deflexed to 1 side at anthesis; petals
cuneate, 1-2.5 cm. long, 0.6-1.8 cm. broad, pale pink to
purplish-pink, deeply bilobed; outer stamens with blue, the
inner with blue or white pollen; caps. straight, 4-sided,
1-2.5 cm. long, 1.5-2 mm. broad, 8-ribbed, sessile or short-
pedicelled. Open places, below 4,000 ft.

2. __Plantago hookeriana__ F. & M. var. __californica.__ (Plantaginaceae).
Villous annual; scapes 5-25 cm. tall, spikes capitate to
short-cylindric, 0.5-2.5 cm. long, dense; sepals scarious-
margined, oblong, 3 mm. long, villous; corolla-lobes spreading,
1-2 mm. long; caps. ellipsoid, ca. 3 mm. high; seeds 2, dull,
brown, 2-2.5 mm. long, finely pitted. Common in dry open
places, below 2,500 ft.

3. __Mimulus guttatus__ Fisch. ex DC. (Scrophulariaceae). Monkey-flower.
Annual or perennial; stems more or less fistulous, stout to
weak, 0.5-10 dm. tall, mostly simple; lvs. oval, rounded to
denticulate or pinnatified-dentate at base, 1-8 cm. long, the
upper sessile, more or less connate, the long-petioled; infl.
more or less racemose; pedicels 2-6 cm. long; calyx campanulate,
glabrous to puberulent, often tinged or dotted with red, inflated
and 1.5-2.5 cm. long in fr., strongly plicate-angled, the lobes
acute and the lower inforling fr. so as partly to close the
orifice, the upper tooth mostly less than 3 times the length
of the others; corolla yellow, usully spotted red, mostly
1.5-4 cm. long, the throat nearly closed by the hairy ridges,
the upper lip with reflexed margins and shorter than spreading
lip; anthers glabrous; stigmas fimbriolate; caps. stipitate,
7-9 mm. long, not dehiscing through septum apex; seeds brown,
oblong, plump, ca. 0.5 mm. long, longitudinally striate.
Exceedingly common in wet places, below 10,000 ft.

4. __Eremocarpus setigerus__ (Hook) Benth. (Euphorbiaceae). Turkey-
mullein; Dove Weed. Annual; stems dichotomously branched from
base, forming dense rounded masses 3-20 cm. high and 5-80 cm.
across; lvs. ovate to suborbicular, 1-6 cm. long, on petioles
ca. as long; male fls. pedicelled, the calyx ca. 2 mm. long;
stamens exserted; pistil pubescent; caps. 4 mm. long; seeds
dark, somewhat variegated, 3-4 mm. long, somewhat ridged.
Common in dry open places, in sandy or heavy soil, mostly
below 2,500 ft., sometimes higher.

5. __Asclepias fascicularis__ Dene, in A. DC. (Asclepiadaceae). Milkweed.

Herbaceous-perennial; the stems several, erect, 5-9 dm. tall, glabrous or sparsely puberulent; lvs. linear to linear-lanceolate, usually in whorls of 3-6, or lower and upper fewer, 4-12 cm. long, 3-10 mm. wide, short-petioled, commonly folded among midrib; umbels several in upper axils, many-fld; peduncles 2-5 cm. long; pedicles slender, 6-15 mm. long; calyx pubescent, ca. 2 mm. long; corolla greenish-white, often tinged purple, the lobes oblong, 4-5 mm. long; hoods ca. as long as stamens, broadly ovate; horns slender, exserted, incurved; follicles smooth, narrow, acuminate, 6-9 cm. long; seeds ca. 6 mm. long, the coma 3 or more cm. long. Frequent as colonies in dry places, mostly below 7,000 ft.

6. **Adenostoma fasciculatum** H & A. (Rosaceae). Chamise. Perennial; diffuse shrub, 0.5-3.5 m. high, with well developed basal burl; bark reddish, subglabrous on the twigs, becoming shreddy with age; stipules small, acute; lvs. linear to narrow-clavate, glabrous, acute, short-petioled, 4-10 mm. long, often resinous, panicles 4-12 cm. long; bracts ca. 1 mm. long; fl-tube green, almost 2 mm. long; sepals barely 1 mm. long; petals ca. 1.5 mm.; ovary obliquely truncate. Common dominate on dry slopes and ridges, below 5,000 ft.

7. **Heteromeles arbutifolia** M. Roem. (Rosaceae). Toyon; Christmas-Berry. Perennial; plant 2-10 m. high, freely branched, with gray bark and tomentulose young branchlets; lvs. elliptical to oblong or lance-oblong, 5-10 cm. long, acute at both ends, rather sharply toothed, dark green above, lighter beneath, glabrous or sparsely tomentulose; petioles 1-2 cm. long; fl-tube ca. 3 mm. high; sepals triangular, 1-1.5 mm. long; petals ca. 4 mm. long; fr. 5-6 mm. long, quite persistent through the winter months; seeds oblong-ovoid, flattened, brown, 2.5-3 mm. long, ca. 1.6-1.8 mm. broad. Common on semi-dry brushy slopes and in canyons, below 4,000 ft.

8. **Pinus sabiniana** Dougl. (Pinaceae). Digger Pine. Tree 12-18(-30) m. high, the trunk dividing and supporting an open sparsely leafy crown; bark dark brown, often tinged purple, with low broad ridges and large brown scales; branchlets stout, at first pale and glabrous, later darker; lvs. in 3's, stout, gray-green, 20-30 cm. long, with many brands of stomates and lasting 3-4 years; male catkins 3-4 cm. long; female cones long-stalked, deflexed, broadly ovoid to subglobose, mostly 15-25 cm. long, light- to chocolate-brown, remaining on trees for some years after shedding seeds, the scales ending in stout flattened downwardly projecting hooks; seeds blackish-brown, 2-24 mm. long, with very short wings. Dry slopes and ridges, below 4,500 ft.

(Munz, 1973)