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Biology of Ultramafic Rocks and Soils: Research Goals for the Future

Robert S. Boyd^{1,*}, Arthur R. Kruckeberg², and Nishanta Rajakaruna³

Introduction

At this, the 6th International Conference on Serpentine Ecology, it seems timely to review briefly the present status of the field and to project the needs for future research. Although a great deal of serpentine research was done prior to 1960, as summarized by Krause (1958) and discussed briefly by Brooks (1987), much of our progress in learning how serpentine geology affects plant and animal life occurred in the mid- to late 20th century. In that era, it was the landmark studies of several scientists worldwide that initiated a meteoric increase in published serpentine research. Key players in setting the stage for this burgeoning output included pioneers in Europe (e.g., John Proctor, Stan Woodell, Ornella Vergnano, and Olof Rune), North America (e.g., Herbert Mason, Robert Whittaker, Hans Jenny, Richard Walker, and Arthur Kruckeberg); and elsewhere (e.g., Robert Brooks, Alan Baker, Roger Reeves, and Tanguy Jaffré). All made notable contributions to understanding the “serpentine syndrome.”

Despite the flourishing of serpentine studies in recent years, there is much “unfinished business.” After all, an axiom of science is that there is an unending quest for answers. In the many subdisciplines of geology and the soil and plant sciences, serpentine areas still hold mysteries—unsolved questions and challenges for the future. We now examine some of them, organized by the five major topic areas covered by the conference (Geology and Soils, Biota, Ecology and Evolution, Physiology and Genetics, and Applied Ecology), and point out how some of the contributions at the conference, and some that are included in this Proceedings Special Issue, address them.

Geology and Soils

Biologists loosely use the term “serpentine” to describe rocks that are referred to by geologists as “ultramafics.” Interpretation of ultramafic geology underwent major changes in the late 20th century. Before the plate tectonics revolution, ultramafics were baffling and often controversial lithological

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mysteries. Today, however, ultramafics play a central role in the interpretation of lithological sequences (ophiolite suites) at tectonic suture zones worldwide. Ultramafic outcrops are now interpreted as originating from upper mantle magma thrust upward to reach the surface of the earth's crust. A recent festschrift volume (Ernst 2004) honors the major contributions of Robert Coleman, Professor Emeritus at Stanford University (California, USA) and contributor to prior International Conferences on Serpentine Ecology (Coleman and Alexander 2004, Coleman and Jove 1992), to this reinterpretation of ultramafic geology.

Knowledge of ultramafic geology and soils is fundamental to serpentine ecology (Alexander et al. 2007), and more information is needed to provide an adequate foundation. Ultramafic rocks and soils are widely but patchily distributed on Earth; they are found on every continent and in every major biome (Harrison and Kruckeberg 2008). Some continents (Australia, Europe, North America) are relatively well-studied, but many other areas (Asia, Africa, South America) are comparatively unknown (at least to the English-speaking world). The 6th Conference illustrated this imbalance, with contributions regarding geology, soils, and plant/soil relations in the Appalachians (USA), California (USA), Newfoundland and Québec (Canada), Albania, Italy, and Puerto Rico. For example, in this Special Issue, D'Amico et al. (2009) describe high-altitude serpentine soils of the Western Alps and explore the correlations between soil metal concentrations and their biological and microbiological activities.

But there were two notable exceptions at the 6th Conference to the usual focus on Europe and North America. In one, a poster by Maria Marta Chavarria Diaz (Area de Conservación Guanacaste, Costa Rica) and Earl Alexander (Soils and Geocology, Concord, CA, USA) presented information on the serpentine geocology of the Santa Elena Peninsula in Costa Rica, thus building upon the pioneering exploration of Reeves et al. (2007) into Costa Rican serpentine sites. The other exception, included in this Special Issue (Cardace and Hoehler 2009), evaluates the ability of the serpentinization process to create habitat capable of supporting microbial life. This latter work is exciting for two reasons. First, the chemical reactions of the serpentinization process may have generated conditions (including energy-containing molecules such as methane or hydrogen) that promoted the evolution of life on Earth (Schulte et al. 2006). Thus, serpentines may have been the very cradle of biology! Second, Cardace and Hoehler (2009) are exploring a similar connection between serpentines and life on other planets, thus potentially taking serpentine ecology into the rarefied atmosphere of interplanetary biology.

Serpentinologists are tempted to divide the world (geological, pedological, and biological) in a binary way: "serpentine" versus "non-serpentine." But both serpentine sites and non-serpentine sites encompass substantial variation, and the importance of this variation can be overlooked in our desire to make generalizations. In particular, biologists and

soil scientists tend to treat peridotite and serpentinite as “serpentine,” but in fact the differences between those rocks may lead to important pedological and biological distinctions. In this volume, Alexander (2009) investigates this question and finds both soil and vegetation differences between these two substrates in the Klamath Mountains of California–Oregon, USA. Further studies that investigate variation in the geological, pedological, and biological characteristics of serpentine areas, and interactions between these categories of characteristics, are needed. In addition, differences in soil characteristics and vegetation between tropical and temperate-zone serpentine soils of similar overall chemical composition are also worthy of more study.

Biota

As pointed out above, our knowledge of serpentine areas varies greatly depending on their geographic location, and this is true for our biological knowledge as well as our knowledge of geology and soils. At the 6th Conference, contributions to our biotic knowledge of serpentine areas included locations in Australia, Bulgaria, Canada (Newfoundland and Québec), Iran, Italy, Japan, New Caledonia, Portugal, Russia, Spain, Sri Lanka, Turkey, and the USA (California, Maryland, Pennsylvania, and Maine). Some of these areas are better-studied than others, but there is a long list of countries for which very little knowledge is available, at least to the English-speaking scientific community. This caveat about the English language is an important point; Brooks (1987) noted that about 30% of the serpentine literature used for his ground-breaking book was written in languages other than English. Thus, we are unsure if our statement above about the lack of knowledge regarding the serpentines of some countries is due to our lack of familiarity with the content of non-English language journals published in those countries. The areas lacking serpentine research published in English includes those countries with rapidly growing global influence, such as China and India, as well as the countries of Central and South America. We hope that future International Serpentine Conferences will include contributions from scientists in these areas to achieve a truly global understanding of serpentine ecology.

An important outcome of each of the six International Conferences in Serpentine Ecology has been the sharing of information between scientists from different countries. In some cases, this sharing has included presenting information in non-English languages (e.g., Jaffré et al. 1997, Boyd et al. 2004). Valuable as well are contributions in which the literature published in one language is made available to readers of another by means of a review written in that other language. A case in point is presented in this Special Issue: the contribution of Mizuno et al. (2009) brings some of the serpentine literature from a non-English speaking country (in this case, Japan) to the attention of Anglophones.

Future investigations that add to our knowledge of the serpentine biota are sorely needed. Basic inventories are lacking for many relatively neglected groups of organisms (e.g., bryophytes, insects, lichens, nematodes, protists), and new species likely await discovery in these groups. As an example, Figure 1 and the cover of this Special Issue show photos of *Melanotrichus boydi* Schwartz and Wall, a new species of mirid bug described in 2001 that is found only on serpentines in the foothills of California's Sierra Nevada (Schwartz and Wall 2001). This species is one of the first discovered "high-nickel insects," species with relatively high levels of Ni in their tissues that are currently known only from serpentine sites (Boyd 2009). Of course, additional information is needed even in better-studied groups, such as the vascular plants, and in relatively well-studied regions such as North



Figure 1. Adult form of the mirid bug *Melanotrichus boydi*, found only on serpentines in the foothills of California's Sierra Nevada. Photograph © R. Boyd.

America. Harris and Rajakaruna (2009) highlight several serpentine endemics for eastern North America (including *Adiantum viridimontanum*; see cover photo) and stress the need for additional surveys to better document the biota of underexplored serpentine barrens of eastern North America.

Hyperaccumulators are fascinating plants that can take up relatively large amounts of an element into their tissues. By now, over 390 taxa are known to be Ni hyperaccumulators (Reeves and Adigüzel 2008), and the vast majority of these grow on serpentine soils; Kazakou et al. (2008) report that 85–90% of Ni hyperaccumulators are serpentine endemics, and the rest occur on other soils but hyperaccumulate Ni when growing on serpentine soil. It is likely that more are to be found in surveys of both temperate and tropical serpentines, and these surveys must continue. At the Conference, Roger Reeves (University of Melbourne, Australia) and Nezaket Adigüzel (Gazi University, Ankara, Turkey) presented an update of their recently published work (Reeves and Adigüzel 2008) documenting Ni hyperaccumulators from the serpentines of Turkey and adjacent areas.

Many studies of serpentine biota use a comparative approach and evaluate both serpentine and non-serpentine study sites. This approach was used by two presentations at the Conference that add to our knowledge of ectomycorrhizal (ECM) fungal communities (Branco 2009) as well as bryophytes (Briscoe et al. 2009). The contribution of Branco (2009), included in this Special Issue, investigates ECM associated with oak forests in Portugal, finding evidence for potentially high fungal endemism in serpentine soils. The bryophyte work of Briscoe et al. (2009), published elsewhere, reports greater bryophyte diversity for serpentine compared to granite on the Deer Isle complex, ME, USA.

Ecology and Evolution

Ecology

Serpentine outcrops often form ecological islands embedded in a matrix of different rock types. Thus, they can be analyzed using the concepts of “island biogeography,” as first outlined by MacArthur and Wilson (1967). The pioneering work of Susan Harrison and colleagues (e.g., Harrison et al. 2006) has examined the California serpentine flora in just such a manner, but more case histories are merited. Additional examples would be desirable, from both temperate and tropical biomes (e.g., the Balkans, Brazil, Cuba, etc.), to determine if different climatic or biogeographic factors in areas other than California result in different biogeographic patterns.

Most serpentine sites worldwide make contact with non-serpentine (“normal”) soil. Often there are noticeable differences in the soil and vegetation (Fig. 2; Rajakaruna and Boyd 2008; see also this volume’s cover photo of contact zone on Mt. Albert, Québec, Canada, taken on the post-Conference field trip) and these differences have stimulated much scientific interest in serpentine ecology. It is ironic, therefore, that these

contact zones themselves are little investigated. What is the plant community structure in such boundary zones? Are their soils intermediate in chemical and physical properties? Does species composition in contact zones differ from that of sites beyond the contact? Is there evidence for hybrid swarms in such contact zones, especially of closely related taxa found on the abutting substrates? We hope that future serpentine conferences will include studies that seek answers to these questions.

Hyperaccumulator plants have received much attention in prior conferences (e.g., Proctor 1999), and this trend continued at the 6th Conference. Much research has focused on the physiology of hyperaccumulators (see section on Physiology below), but the ecological interactions of hyperaccumulators with other organisms are also being investigated. In recent years, interaction ecology (plant-animal, plant-plant, etc.) has gained major research attention. For serpentines, Robert Boyd and colleagues have studied the impacts of Ni hyperaccumulation on species interactions in serpentine communities. This work initially focused on plant interactions with natural enemies, arguing that hyperaccumulation of metals could defend plants against these natural enemies (see review from proceedings of the 5th Conference: Boyd 2007). It has expanded to explore other interactions, including antagonistic plant-plant interactions (elemental allelopathy: see review by Morris et al. 2009) and plant-decomposer interactions (Boyd et al. 2008a). In this Special Issue, Boyd et al. (2009a) explore the impact of hyperaccumulation on a commensal plant-plant interaction, showing that bryophytic epiphytes in a New Caledonian humid forest have greater Ni concentrations when they grow on Ni-hyperaccumulator host plants. They also show that some of these bryophytes are themselves Ni hyperaccumulators (as defined by the levels of Ni in the collected samples).

Many serpentine studies contrast serpentine and non-serpentine sites, but as mentioned above, there is considerable ecological variation within serpentine sites (Rajakaruna and Bohm 1999). Well known is the substantial variation in chemical content (Ni, Ca/Mg, etc.) of serpentine soils.

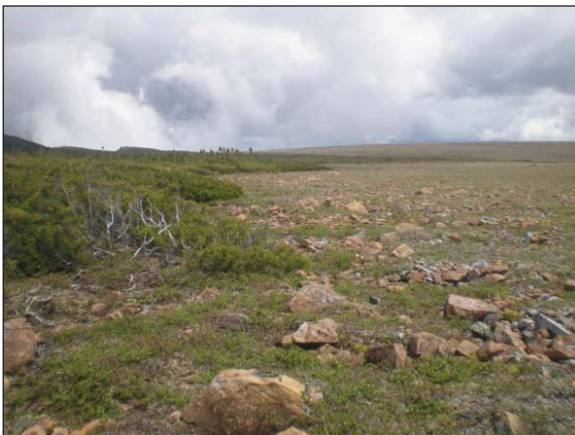


Figure 2. Contact zone between amphibolite (on the left) and serpentine (on the right) at Mont Albert in Quebec, Canada. Note the strong vegetation differences. Photograph © Ryan O'Dell.

Examination of differences in species composition caused by differences in soil chemistry would be desirable. A poster by Jennifer Doherty and Brenda Casper (University of Pennsylvania, USA) explored arbuscular mycorrhizal fungal (AMF) community diversity and how that diversity may affect performance of serpentine grasses in heterogeneous serpentine soils. The Casper lab is evaluating the role of AMF in plant-soil feedback (defined as influences of a plant on soil properties that can affect the next plant to occupy the same site) in Pennsylvania serpentine grasslands (e.g., Casper and Castelli 2007), finding that both feedback and plant-plant competition interact in structuring these communities.

Evolution

Understanding plant adaptations to the “serpentine syndrome” has been an important focus of serpentine ecologists for at least a half century. Years ago, Anthony Bradshaw (Liverpool University, UK) found that certain taxa from normal soils had the potential of incipient tolerance to soils with high concentrations of heavy metals (Gregory and Bradshaw 1965). Such pre-adaptation may also exist in taxa bordering serpentine sites. Simple germination tests on serpentine soils could reveal preadaptation in certain taxa. It may be proposed that such partial tolerance could be an initial step towards ecotypic formation and subsequent speciation. Genera in certain tolerance-prone families could be tested, e.g., *Alyssum* (madwort), *Streptanthus* (jewelflower), *Arabis* (rockcress), *Thlaspi* (pennycress), and other genera in the Brassicaceae, and in the Caryophyllaceae, genera like *Silene* (catchfly), *Minuartia* (sandwort), and *Dianthus* (pink). Asteraceae and Poaceae are also likely sources of testable taxa. Past studies have demonstrated that wide-ranging species often have serpentine-tolerant and intolerant races. Nearly all such cases have involved herbaceous genera. Yet to be tested are woody species with serpentine and non-serpentine populations. Just for California, genera like *Adenostoma* (chamise), *Arctostaphylos* (manzanita), *Ceanothus* (ceanothus), *Umbellularia* (California laurel), *Heteromeles* (toyon), and *Garrya* (silktassel) provide likely candidates for testing. Although many taxa in these woody genera have long been considered as indifferent to substrate, only common garden, ecophysiological, and genetic studies can confirm if there is genotypic differentiation across substrate.

Studies of serpentine floras have noted “serpentinomorphoses,” morphological differences between populations or taxa growing on serpentine and non-serpentine soils (Kruckeberg 2002). These often include seromorphic features such as sclerophylly, reduced stature, and increased root:shoot ratios (Kruckeberg 2002). At the 5th Conference, held on the serpentine-rich island of Cuba, the contributions of our Cuban colleagues (e.g., Bécquer Granados et al. 2004, Ferrás Alvarez et al. 2004) made plain this interesting observation and also that the influence of serpentine environments on plant form needs more study. What are the contributions of phenotypic plasticity versus genetic traits to serpentinomorphoses? Exactly what are the

ecological functions of serpentinomorphoses and how important are they to adaptation to serpentine soils? In this Special Issue, Pavlova (2009) documents variation between serpentine and non-serpentine populations of *Teucrium chamaedrys* L., and Boyd et al. (2009b) explore morphological and elemental concentration variation among populations of the serpentine endemic Ni hyperaccumulator *Streptanthus polygaloides* Gray. We hope that future Conference contributions will explore the evolutionary and ecological ramifications of the variability documented by these and other studies of serpentine plants.

How serpentine endemic species have evolved has tantalized botanists for decades (Kruckeberg 1986, Rajakaruna 2004). Do they evolve directly from non-tolerant species or from species that are already serpentine tolerant? At the Conference, Brian Anacker et al. (University of California, Davis, CA, USA) used molecular phylogenies to test whether serpentine endemic taxa arise along a directional evolutionary pathway of non-tolerator to tolerator to endemic. They reported several cases of significant directionality along this hypothesized pathway, thus supporting this general model.

For areas already well inventoried, it would be desirable to determine the relative ages of serpentine endemics. Are some taxa paleoendemics and others neoendemics? The working hypotheses for ages of taxa are as follows (Kruckeberg 2002): paleoendemics have no close relatives on nearby non-serpentine sites; e.g., *Darlingtonia californica* Torr. (California Pitcherplant) and *Kalmiopsis leachiana* (L.F. Hend.) Rehder (North Umpqua Kalmiopsis). Neoendemics are thought to have close relatives on nearby normal soils: e.g., California genera like *Layia* (tidy-tips), *Streptanthus* (jewelflower), *Gilia* (gilia), and *Phacelia* (phacelia). These hypotheses need verification, and the work of Anacker et al. presented at the Conference provided an initial test; for their dataset from 20 genera, they found few endemic lineages more than 10 million years old, suggesting that paleoendemics are relatively rare. While this may be the case for the flora of California, it is important to repeat such analyses, as phylogenies become available, for other serpentine floras around the world.

Molecular phylogeny provides a unique protocol for testing and establishing species relationships. As yet it has been little used to determine linkages within genera having species on serpentine and normal soils (but see Baldwin 2005). Nearly every serpentine flora, temperate and tropical, has genera and families suitable for phylogenetic verification. Among temperate genera, *Alyssum*, *Streptanthus*, *Thlaspi*, and *Phacelia* would be worth testing. Numerous genera found on serpentines of Cuba, New Caledonia, and South Africa could be subjects for molecular phylogenetic study. Phylogenetic analysis has been used to examine evolution of Ni hyperaccumulation in *Alyssum* (Mengoni et al. 2003), serpentine tolerance in *Calochortus* (mariposa lily; Patterson and Givnish 2004), and in angiosperms in general (Broadley et al. 2001), and similar approaches could be used to assess patterns of serpentine endemism.

Physiology and Genetics

Physiology

Questions still abound in the area of functional accommodation of plants to serpentine soils. The question of Ca/Mg levels still provokes inquiry (Kazakou et al. 2008). Is low Ca the major factor? Is high Mg a major player in serpentine tolerance? It is not unlikely that species are more sensitive to either low Ca or high Mg. Additionally, what is the importance of stresses due to metals such as Co, Cr, and Ni? Given that a multiplicity of traits—chemical and physiological—constitute Jenny's "serpentine syndrome," experimental verification of serpentine tolerance will be complex. A recent investigation (Oze et al. 2008) of elemental uptake into vegetation on serpentine and non-serpentine (chert) soils suggested that elemental uptake discrimination by roots is an important mechanism by which serpentine species tolerate serpentine soil chemistry. It is likely that ecological as well as physiological factors will be intertwined. For example, Springer et al. (2007) showed that the susceptibility of *Hesperolinon californicum* Benth. (Small) (California Dwarf-Flax; a species found both on and off of serpentine) to the rust fungus *Melampsora lini* Persoon (Flax Rust) was negatively correlated with soil Ca levels, suggesting that pathogen pressure on serpentine soils would be more intense.

Major questions also abound at cellular and molecular levels. Mineral uptake, translocation, or mineral exclusion must involve particular cellular mechanisms (ATPases, protein transporters, etc.). Though progress has been made in this area, further exploration of cellular/molecular mechanisms is surely called for. At the 6th conference, there were few contributions from scientists working in this area. One presentation, by Jola Mesjasz-Przybylowicz and colleagues (iThemba Labs, South Africa), was unique in that it examined Ni-elimination strategies by beetles feeding on a Ni-hyperaccumulator plant, *Berkheya coddii* Roessler, from the serpentines of South Africa. It was encouraging to see adaptive questions being asked regarding serpentine animal species and thus broadening the focus from plants to other serpentine biota. In this same vein, a poster presentation by Sonia Costa and colleagues from the University of Coimbra, Portugal, examined mycorrhizal colonization of a serpentine grass species as affected by Ni and soil fertility, thus including plant-fungal interactions in this physiological session.

A most tantalizing conundrum in the area of mineral flux has to do with Ni hyperaccumulation. Even though the number of Ni hyperaccumulators is impressive (>390 taxa), many serpentinophytes either exclude Ni from uptake or do not reach the hyperaccumulation threshold (>1000 mg Ni kg⁻¹ in dry leaf tissue). Foremost is the question: how do most serpentine plants prevent Ni uptake? This has to be a genetically fixed, adaptive trait. Answers are likely to come from cellular and molecular methods. These approaches are being used to determine the genetic bases and molecular pathways of

hyperaccumulation; see the recent review by Verbruggen et al. (2009) for an overview of our current understanding. Then, those taxa that can take up Ni below the hyperaccumulation level pose other questions. Are these taxa on the way to becoming hyperaccumulators? It can be hypothesized that those few moderate Ni accumulators reveal the intermediate stages that Ni hyperaccumulators could have gone through during their evolution. Boyd (2007), proposing that defensive effects may be a selective force favoring survival of plants with still higher Ni concentrations, called this the “defensive enhancement” hypothesis for the evolution of elemental hyperaccumulation. Evidence regarding this hypothesis is needed, and a presentation at the conference of research by Sarah Dalrymple et al. (University of California, Davis, CA, USA) showed that as little as 40 mg Ni kg⁻¹ in shoots of *Mimulus guttatus* DC (Seep Monkey Flower) reduced damage by caterpillar herbivores, suggesting defensive effects of Ni at concentrations far less than hyperaccumulator levels.

Several contributions in this Special Issue address other questions regarding hyperaccumulation. Ghaderian et al. (2009) add to the extensive early work of Homer et al. (1991) on metal uptake by *Alyssum* Ni hyperaccumulators. Ghaderian et al. (2009) examine the ability of an Iranian Ni hyperaccumulator (*Alyssum bracteatum* Boiss. and Buhse) to accumulate Co, finding that plants from a serpentine population accumulate more than those from a non-serpentine population. They also show Co hyperaccumulation is possible when plants are grown in an artificial medium, suggesting that Ni and Co uptake and sequestration abilities are correlated. Pollard et al. (2009) investigate the ability of a non-serpentine species (*Phytolacca americana* L. [Poke Sallet]) to take up Mn. They find that, under hydroponic conditions, plants hyperaccumulate Mn even though no cases of hyperaccumulation have been reported from plants in the field. They thus document what Boyd and Martens (1998) termed “latent hyperaccumulation,” the physiological ability of a species to hyperaccumulate that is not detected by studies of field-collected samples. Field-collected samples are part of the definition of hyperaccumulation (see Reeves 1992), but Pollard et al. (2009) show that there may be more species of plants with hyperaccumulation abilities than we had thought. Boyd and Jaffré (2009) examine the influence of leaf age on Ni concentration in New Caledonian serpentine species, including species that cover a wide range of leaf Ni levels. They report that leaves generally do not vary significantly in Ni levels as they age. They also suggest use of a new term (hemi-accumulator) to categorize plants with Ni levels in the range of 100–1000 mg Ni kg⁻¹ (in dry leaf tissue), to complement terms currently in use for plants with <100 mg Ni kg⁻¹ (non-accumulator), 1000–10,000 mg Ni kg⁻¹ Ni (hyperaccumulator), and >10,000 mg Ni kg⁻¹ (hypernickelophore). Finally, Mesjasz-Przybyłowicz et al. (2009) study the ultrastructure of roots of the South African Ni hyperaccumulator *Senecio coronatus* (Thunb.) Harv. This species is unusual because some serpentine

populations hyperaccumulate Ni whereas others do not (Boyd et al. 2008b); only a few Ni-hyperaccumulator species show this variation in Ni hyperaccumulation (Kazakou et al. 2008). Mesjasz-Przybylowicz et al. (2009) report several differences, including differences in the Casparian strips, that may help explain the ability of the non-hyperaccumulator to limit Ni uptake from serpentine soil.

Genetics

The long-standing question of the genetic basis for serpentine tolerance has yet to be fully resolved: is tolerance controlled by a single or few genes or is it polygenic? Approaches to solving this question could involve breeding tests, DNA analyses, and other techniques. For example, the Toby Bradshaw lab (University of Washington, Seattle, WA, USA) is exploring this question (Brady et al. 2005) for species in the genus *Mimulus* (monkey flower) using quantitative trait loci (QTL). The evolutionary ecology of serpentine endemism is also the target of “serpentinomics,” the application of genomic techniques to analyze local adaptation (Wright and von Wettberg 2009). Wright and von Wettberg (2009) present their efforts to detect molecular convergence among multiple *Collinsia sparsiflora* Fisch. & C.A. Mey. (Spinster's Blue-eyed Mary) populations that have adapted to serpentine soils. This work builds on initial work that used F2 hybrids to analyze patterns of local adaptation and selection on serpentine and non-serpentine populations of this species (Wright and Stanton 2007). Genomic tools are also important to discern relations among the microbe populations found on and off of serpentine soils. A recent study employs such tools to explore patterns of microbial diversity and biogeography across serpentine and non-serpentine substrates (Oline 2006).

We mentioned previously the general lack of ecological information regarding serpentine/non-serpentine contact zones, and genetic questions regarding these zones have also not yet been explored. For example, how much and to what effect does gene flow into or from serpentine and normal soils have on populations on either side of the edaphic boundary? Techniques exist for facilitating such studies: aerial insect transmission of tagged pollen, marker genes in either population, or detection of enhanced serpentine tolerance in neighboring non-serpentine populations.

Applied Ecology

The effects of human activities on serpentine sites have been substantial and have worked reciprocally. Serpentine sites have impacted humans, and even more so, human intrusions on ultramafics have gone on for centuries (Kruckeberg 2002). There are several research directions needed here. Physical alteration of serpentine sites (mining, logging, fire, etc.) post still unresolved issues. Can disturbed serpentine sites be restored, especially by planting tolerant plant stock? How do native species on serpentine sites react to disturbance?

Some species may increase under disturbance, while others decrease or even become extinct. Revegetation of disturbed serpentine sites has been an important theme in past conferences; for example, the proceedings of the 2nd International Conference (Jaffré et al. 1997) contained an entire section of nine papers dedicated to this topic. In this Special Issue from the 6th Conference, O'Dell and Claassen (2009) provide a review of the concepts involved in revegetating disturbed serpentine sites. Their paper is a helpful summary of the literature in this applied area of serpentine ecology. A specific environmental hazard associated with some serpentine sites is that associated with asbestos. Favero-Longo et al. (2009) report results from using native plants to reduce the hazards of airborne asbestos fibers originating from a closed serpentine mining site. They find that plant cover significantly reduces the hazard and provide an example of how successful revegetation can yield important environmental benefits.

The growing human population of the planet drives humanity to consider ways to generate new arable land. Can serpentine habitats be brought into productive agriculture? Because of the challenges of the “serpentine syndrome” for plant growth, these areas are not often used for traditional crops. Yet some crops are grown successfully on managed serpentine soils (e.g., growing wine grapes on serpentine alluvial soils in California). Our understanding of the “serpentine syndrome” and its effects on plants may suggest agricultural strategies that can put some serpentine soils into agricultural use. A non-traditional agricultural technique that may use plant species native to serpentine is phytomining (Nicks and Chambers 1998). For example, in this technique, a Ni hyperaccumulator would be cultivated on serpentine soils, harvested, and processed into ore for its Ni content. Some initial tests of the feasibility of this technology have been conducted (e.g., Brooks et al. 2001). A kindred use of serpentine species is in the field of phytoremediation (Raskin and Ensley 2000, Pilon-Smits 2004). Barely tested is the possibility of using hyperaccumulators to extract metals from contaminated sites (Rajakaruna et al. 2006). These extracted metals could then be processed into ore as in phytomining, or even be useful as food supplements in the case of Zn (Mayer et al. 2008), since Zn is an important dietary micronutrient. However, from the conservation perspective, it is critical that such phytomining operations are established on degraded serpentine landscapes rather than on pristine habitats.

Conservation of serpentine biota is another important area of concern (Rajakaruna et al. 2009). The need for conservation of these unique areas was recognized at the First International Conference on Serpentine Ecology, held in 1991 at the University of California, Davis, CA, USA. The 70 delegates to that conference approved a resolution calling upon governments, public and private agencies, and private industry to take steps to protect the biodiversity contained in serpentine areas (Kruckeberg 1992). This call has been repeated since then (e.g., Whiting et al. 2004) and remains an area in need of close attention.

A major problem in conservation biology is the impact of non-native invasive species on natives (Terrill 2007), and disturbed serpentine sites can be invaded by weedy species of non-serpentine origin. There is some evidence (Harrison et al. 2003) that serpentine habitats have fewer non-native plant species, presumably because they are challenging media for plant growth. Are successful non-native invasive species ones that are already genetically tolerant, either by possessing a general-purpose genotype or by rapidly evolving tolerance? And how do other anthropogenic changes alter the invasibility of ultramafics? For example, recent studies (Weiss 1999, Zavaleta et al. 2003) show that vehicle emissions have resulted in N-enrichment of serpentine soils near major California highways. This enrichment may allow non-native species to invade these ultramafic sites by alleviating N limitation in these soils. A similar but important area of research should focus on multiple nutrient and other element enrichment via atmospheric sources. The deposition of other nutrients such as P and Ca and various pollutants can also have drastic impacts on the unique soil chemistry and resulting biotic interactions of serpentine habitats.

Climate change is predicted to affect the planet's biota in major ways (Loarie et al. 2008, Thomas et al. 2004), and recent analysis (Solomon et al. 2009) suggests it may be irreversible on a timescale of a millennium or so. Edaphically restricted communities such as those on serpentine sites will be affected as well. But will the features that make them unique, such as their insular nature and their biogeochemical/biological distinctiveness, make them more or less susceptible to disruption by climate change? Harrison et al. (2009) propose a conceptual model to test this question and are gathering long-term comparative data to provide initial answers. Additional studies in other geographic regions would be helpful; in particular, the history of scientific interest in European serpentine areas (Brooks 1987) may allow for other long-term datasets to be generated there. In the context of serpentine endemism, we speculate that narrow endemics are more liable to extinction due to climate change. Since some narrow endemics are already endangered by their limited ranges, climate change will likely increase their chances of extinction.

A major driver of climate change is carbon emissions into the atmosphere (Hansen et al. 2008, Solomon et al. 2009). Given the potential threat of climate change to the serpentine flora, it is ironic that serpentine sites may offer a partial solution to climate change by providing a mechanism for carbon sequestration. Extremely Mg-rich rock, such as olivine or serpentine, can react with water and carbon dioxide to form magnesium carbonate plus silica, thus sequestering potentially damaging carbon dioxide emissions (Maroto-Valer et al. 2005). This technique is under investigation (see review by Yang et al. 2008), but it is unclear how its large-scale application might impact the biota of serpentine areas. If the overall history of human impacts on Earth's habitats is any guide, this partial solution to climate change could severely impact serpentine sites used to implement this technology. It would be tragic

to be forced to degrade the biodiversity of serpentine sites in order to help save biodiversity on a planetary scale. As we mentioned earlier, scientists have speculated that serpentine vents may have been involved in the initial evolution of life on Earth. It would be an irony of cosmic proportions if the biota of present-day serpentine sites were to be sacrificed in order to help save the life formed on Earth billions of years ago during serpentinization!

Summary

By the early 21st century, studies on the geology and biology of ultramafics have become a significant focus in the natural sciences. Yet inevitably, the burgeoning fields of research have unearthed yet more unresolved questions. Our mission here has been to describe some of the challenges awaiting future research and some of the contributions made during the 6th International Conference on Serpentine Ecology. We hope that the 7th International Conference (scheduled for 2011 and hosted by the University of Coimbra in Portugal) will be as successful as the 6th (and prior) Conferences were in advancing our knowledge of these fascinating areas. Certainly, the new generation of serpentinophilic scientists has a full palette from which to choose their research questions!

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