Plant Science 217–218 (2014) 8–17

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

Facultative hyperaccumulation of heavy metals and metalloids

A. Joseph Pollard [a,*], Roger D. Reeves [b], Alan J.M. Baker [c]

[a] Department of Biology, Furman University, Greenville SC 29613, USA
[b] Palmerston North, New Zealand
[c] School of Botany, The University of Melbourne and Centre for Mined Land Rehabilitation, University of Queensland, Australia

ARTICLE INFO

Article history:
Received 16 August 2013
Received in revised form
15 November 2013
Accepted 16 November 2013
Available online 23 November 2013

Keywords:
Hyperaccumulation
Facultative
Constitutive
Pseudometallophyte
Serpentine
Metal tolerance

ABSTRACT

Approximately 500 species of plants are known to hyperaccumulate heavy metals and metalloids. The majority are obligate metallophytes, species that are restricted to metalliferous soils. However, a smaller but increasing list of plants are "facultative hyperaccumulators" that hyperaccumulate heavy metals when occurring on metalliferous soils, yet also occur commonly on normal, non-metalliferous soils. This paper reviews the biology of facultative hyperaccumulators and the opportunities they provide for ecological and evolutionary research. The existence of facultative hyperaccumulator populations across a wide edaphic range allows intraspecific comparisons of tolerance and uptake physiology. This approach has been used to study zinc and cadmium hyperaccumulation by *Noccaea* (*Thlaspi*) *caerulescens* and *Arabidopsis halleri*, and it will be instructive to make similar comparisons on species that are distributed even more abundantly on normal soil. Over 90% of known hyperaccumulators occur on serpentine (ultramafic) soil and accumulate nickel, yet there have paradoxically been few experimental studies of facultative nickel hyperaccumulation. Several hypotheses suggested to explain the evolution of hyperaccumulation seem unlikely when most populations of a species occur on normal soil, where plants cannot hyperaccumulate due to low metal availability. In such species, it may be that hyperaccumulation is an ancestral phylogenetic trait or an anomalous manifestation of physiological mechanisms evolved on normal soils, and may or may not have direct adaptive benefits.

Contents

* Corresponding author. Tel.: +1 864 294 3244; fax: +1 864 294 2058.
E-mail address: joe.pollard@furman.edu (A.J. Pollard).

0168-9452/$ – see front matter © 2013 Elsevier Ireland Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.plantsci.2013.11.011

1. Introduction

The interaction of plants with toxic metal and metalloid elements in soils has been used as a productive model for physiological, ecological, genetic and evolutionary research for over half a century. Although many such elements are essential micronutrients, most are toxic at high concentrations. The early studies in this field focused on tolerance mechanisms that allow some plants to grow in metal-contaminated soils where most species cannot survive [1]. More recent interest has centered on a small subset of these plants that not only tolerate metals, but also concentrate them to exceptional concentrations in their leaves, the phenomenon of hyperaccumulation [2,3]. Both tolerance and hyperaccumulation may have commercial applications, whether for revegetation of contaminated soils (phytostabilization), for extraction of metals for their intrinsic value (phytomining), or for plant-based remediation of polluted soils (phytoextraction) [4,5].

This review focuses on metal hyperaccumulator species that occur naturally on both metalliferous and non-metalliferous soils. Such species may broadly be described as facultative hyperaccumulators, a classification which will be explained more fully in Section 2.1. Facultative hyperaccumulators make up a minority of the known hyperaccumulator species and in general have been poorly studied, yet they also include a few of the most thoroughly investigated research models for metal tolerance and uptake. This paper does not attempt to comprehensively describe the biology of hyperaccumulation or its underlying genetics and physiology, which have been surveyed in other recent reviews [*e.g.* 2,3,6,7]. Instead, we will concentrate on the unique features of facultative hyperaccumulators. We will argue that ecological and evolutionary hypotheses regarding hyperaccumulating plants are expected to depend strongly on the biogeographic patterns of hyperaccumulator distribution, whether obligately restricted to metalliferous soils, primarily on metalliferous soils and occasionally on other substrates, or primarily on non-metalliferous soils but occasionally on metalliferous ones where they hyperaccumulate.

2. Defining and describing hyperaccumulators

A recent critique [7] has attempted to clarify, refine and update the definition of metal hyperaccumulation. To paraphrase its conclusions, a hyperaccumulator can be defined as a plant whose leaves contain a metallic element at a concentration exceeding a specified threshold, when growing in nature (not in experimental cultivation). The threshold concentration should be 2–3 orders of magnitude higher than in leaves of most species on normal soils, and at least one order of magnitude greater than the usual range found in plants from metalliferous soils. Based on these concepts, the proposed nominal threshold criteria (all in units of μg metal per g of dry leaf tissue) are: 100 for Cd, Se and Tl; 300 for Co, Cr and Cu; 1000 for As, Ni and Pb; 3000 for Zn and 10,000 for Mn [7]. High concentrations of Al have also been reported in several species [8] but it is not clear that accumulation of major soil elements is a comparable phenomenon to hyperaccumulation of trace elements [7], so it will not be considered further in this review. The stipulation that these threshold concentrations should occur in plants growing in nature does not exclude weeds of anthropogenic habitats, but does imply that hyperaccumulators must possess sufficient metal tolerance to maintain a self-sustaining population in metalliferous soils.

Based on the above criteria, approximately 500 taxa have been proposed as hyperaccumulators of one or more metals; thus, hyperaccumulation is a rare phenomenon known in less than 0.2% of the world's inventory of vascular plants [7]. Of the known hyperaccumulators, a huge majority (>450 taxa) are hyperaccumulators of nickel, generally occurring on serpentine (ultramafic) soils. Documented cases of hyperaccumulation of other metals are much rarer. This rarity, combined with their potential for practical application and commercial value, is a strong justification for basic biological studies.

2.1. Biogeographic patterns: obligate and facultative

Hyperaccumulators make up a subset of the category known as metallophytes, plants that occur on metal-enriched soils. Early studies on such plants generated a confusing, redundant and overlapping terminology to describe the biogeographic distribution of metallophytes [1,9,10]. Species that occur exclusively on metalliferous soils have been variously described by the terms indicator, endemic, bodenstet, eumetallophye, absolute metallophyte, strict metallophyte, or obligate metallophyte. Species known to occur on both metalliferous and non-metalliferous soils have been termed bodenvag (meaning "soil-wandering"; alternative spellings include bodenwag and bodenwaag) species, pseudometallophytes and facultative metallophytes. We will consistently employ the adjectives obligate and facultative when describing whether or not a species is restricted to metalliferous soils. For the sake of simplicity, we will use the phrase "normal soils" to imply those which are not unusually enriched in metallic elements, recognizing that this is a gross oversimplification of potential variations in soil structure, texture, chemistry and hydration unrelated to metal concentration.

One early attempt at ecological classification of metallophytes further subdivided the facultative species into three categories: (a) "elective pseudometallophytes", occurring primarily and with greatest vigor on metalliferous soils; (b) "indifferent pseudometallophytes", growing indiscriminately and equally well on metalliferous and normal soils; and (c) "accidental pseudometallophytes", represented by weeds and ruderals appearing sporadically and with reduced vigor on metal-contaminated soils [1,8]. Although this classification has not been widely adopted, it serves as a reminder that the single term "facultative" encompasses a range of biogeographic patterns, ecological relationships and physiological responses.

Most plants that survive on metalliferous soils do so by excluding metals from their shoots [2,7]. In contrast, hyperaccumulators make up only a small subset of metallophytes. Nonetheless, the terms obligate and facultative can be applied to hyperaccumulators to describe their fidelity to metalliferous soils. Because the phrase "hyperaccumulators that are facultative metallophytes" is long and unwieldy, we propose the more compact label "facultative hyperaccumulators", the full meaning of which will be explored throughout this review. One of the first publications to describe facultative hyperaccumulation was a study of *Rinorea bengalensis* from Southeast Asia [11], and the first to systematically categorize obligate and facultative hyperaccumulators across a whole flora appears to have been a series of botanical surveys on the extensive serpentine soils of Cuba [12,13, and references therein]. As with facultative metallophytes in general, the distributions of facultative hyperaccumulators are expected to vary, from species that occur primarily on metalliferous soils, to species that rarely do.

A somewhat different type of variation is occasionally found, in which a species growing on metalliferous soils includes some populations or genotypes that hyperaccumulate metals, and others that do not. Possible examples include *Senecio coronatus* [14] and *Pimelea leptospermoides* [15]. This phenomenon might be termed "erratic hyperaccumulation". Because the plants involved are all obligate metallophytes, we regard it as fundamentally different from facultative hyperaccumulation and will not discuss it further in this review. Little is known about why it occurs, in any case.

Some studies have claimed to identify hyperaccumulator species that are not metallophytes at all, in that they are not