THE ECOPHYSIOLOGY OF PLANT-PHOSPHORUS
INTERACTIONS
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Aims & Scope:

The Springer Series in Plant Ecophysiology comprises a series of volumes that deals with the impact of biotic and abiotic factors on plant functioning and physiological adaptation to the environment. The aim of the Plant Ecophysiology series is to review and integrate the present knowledge on the impact of the environment on plant functioning and adaptation at various levels: from the molecular, biochemical and physiological to a whole plant level. This series is of interest to scientists who like to be informed of new developments and insights in plant ecophysiology, and can be used as advanced textbooks for biology students.

The titles published in this series are listed at the end of this volume.
The Ecophysiology of Plant-Phosphorus Interactions

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The Ecophysiology of Plant-Phosphorus Interactions is the seventh volume in the Plant Ecophysiology series. It reviews the current state of knowledge, concepts and research of plant-phosphorus interactions in natural and managed ecosystems together with aspects of the phosphorus nutrition of crop plants, addressing in particular the sustainability and possible environmental consequences of agricultural production.

Phosphorus (P) is an essential macronutrient for plant growth. Plants take up P as phosphate (Pi) from the soil solution. Since little Pi is available to plants in most soils, they have evolved mechanisms to acquire and use P efficiently and foster symbiotic relationships to help them acquire P sources beyond their immediate range. Whilst in agricultural systems P limitations are frequently overcome by the application of P-fertilizers, these may cause environmental pollution and the use of inorganic Pi is unsustainable. The genetic and phenotypic variation among plants adapted to ecosystems with low P availability provides an opportunity to improve our understanding of plant responses to P limitation and this knowledge could be utilized to develop crop varieties with better P use for agriculture.

In the first chapter of this volume, Holm Tiessen places P in a global context. He reviews the geochemistry of P, the cycling of P in the environment, the effects of humans on P cycles, and their consequences. Next, Karl Niklas describes the allometric relationships between tissue C, N and P concentrations among and within plant species, and explores the implications of these for various physiological, ecological and evolutionary phenomena. Gabrielle Thiébaut explains how P is acquired by aquatic plants and how P supply and seasonal fluctuations in P loads affect the abundance and distribution of aquatic plant species, while Philip White and John Hammond summarize the requirements and functions of P in terrestrial plants and the impacts of P availability on their ecology. These authors also introduce the biochemical, physiological and morphological traits that enable terrestrial plants to acquire and utilize P most effectively, and how the expression of these traits might be regulated by plant P status.

Jonathan Lynch and Kathleen Brown focus on the root traits that provide an adaptive strategy for P acquisition by terrestrial plants, which include: greater root biomass allocation, changes in root architecture to exploit local P patches, increased root length density, proliferation of root hairs, symbiosis with mycorrhizal fungi and the secretion of organic acids and phosphohydrolases. This theme is continued
by Carroll Vance, who addresses the adaptations for the acquisition and use of P in plants lacking effective mycorrhizal symbioses, concentrating on species that develop specialized complex roots (cluster and dauciform) and on Arabidopsis. These chapters are complemented by those of Jose Barea and colleagues, who describe the nature of plant-mycorrhizal symbioses and their impact on plant productivity, plant community structure and P cycling in the environment, and of Petra Marschner, who provides an overview of the influence of rhizosphere microorganisms on the growth and P nutrition of plants. These chapters describe the major influence of plant species on rhizosphere community composition, and discuss the possible reasons for this. They also discuss the use of microbial inoculants to improve plant productivity.

The role of P-fertilizers in agriculture is reviewed by Ernest Kirkby and Johnny Johnston, who emphasize the necessity of P-fertilizers for crop production and reflect on their environmental and ecological footprint. Against the backdrop of depleting Pi reserves, and the necessity for global food security, they establish strategies for more efficient use of soil and fertilizer P based on knowledge of the behavior of P in soils, the introduction of best management practices and the potential for developing “P-efficient” cultivars of crop plants. These strategies are further explored in chapters by John Hammond and Philip White, who describe how the application of P-fertilizers to crop plants can be optimized by monitoring and modeling the P status of soils and plants, and by Tim George and Alan Richardson, who describe how appropriate breeding and transgenic approaches can be used to improve crop P acquisition. The volume concludes with a thought-provoking perspective by John Raven on the past and future P-nutrition of plants, which includes a checklist of priorities for immediate action to enable the world to feed its burgeoning human population.

It is hoped that this book will be of interest to students and researchers studying all aspects plant-phosphorus interactions: omicists, physiologists, ecologists and all readers interested in sustainable crop production.

John P. Hammond
Philip J. White
Chapter 1
PHOSPHORUS IN THE GLOBAL ENVIRONMENT

Holm Tiessen

INTRODUCTION

Phosphorus is not one of the “global” elements, it does not enter the atmosphere like nitrogen, it does not spread like sulfur by acid rain and its solubility in water is so low that there is only a slow, steady movement of P down-stream as landscapes erode and weather, or P-containing pollutants are discharged. Yet, there are some global trends in the distribution of P. To understand these and their drivers it is useful to review some of the basic properties of P in the environment.

The earth’s crust contains about 1,200 mg P kg⁻¹, making it the 11th most abundant element. Common concentrations for total P in soils are between 200 and 800 mg kg⁻¹, with older soils containing lower amounts of P and younger soils containing higher amounts of P. In primary rocks and young soils, P is largely bound to calcium or magnesium, giving P a typical water solubility near 0.5 mg P L⁻¹. The weathering of minerals changes the solubility of P, as Ca is preferentially leached out, the relative abundance of Fe and Al increases and the solubility of P becomes controlled by Fe- or Al-phosphates, which have much lower solubilities than Ca-phosphates. As a result, the sequestration of P in low-solubility Fe and Al-phosphate compounds and the effect of leaching and erosion, many older and tropical soils are P deficient, i.e. the availability of P to plants and other organisms restricts ecosystem processes such as N fixation or C sequestration.

The availability of P to plants is controlled by physical and chemical reactions, including sorption/desorption and precipitation/dissolution and biological processes such as immobilization (uptake by plants and microorganisms) and by mineralization (decomposition of residues). The sorption of P, followed by slower transformations, such as solid state diffusion into the matrix of the sorbent, reduce the solubility of P, sometimes to such a degree that P is said to become “fixed”. Strictly speaking, P fixation is a misnomer, since all chemical reactions are to some degree reversible, but the amount and rate of release of “fixed” P may be so low that they are ecologically insignificant.

Over 99% of naturally occurring P is in the form of phosphate, either as inorganic phosphates or as organic phosphate esters. With its four oxygen atoms per P, phosphate has a high negative charge density, so it can readily bond to any positively charged
cation or surface. This greatly restricts the mobility of P in the environment. When phosphate is bound into relatively large organic molecules, this charge is somewhat shielded. Consequently, organic forms of P are often more mobile in the environment than inorganic P. In most soils organic P accounts for 30–65% of the total P, although some soils contain up to 90% organic P (Harrison 1987). This accumulation of organic P implies low mobility, which is due to the sequestration of P in recalcitrant soil organic matter. The negative relationship between mobility and accumulation of organic P forms is seen in the abundance of inositol hexaphosphate, which may account for half the identifiable organic P in soils. Inositol hexaphosphate is sorbed more strongly than inorganic phosphate in soils due to the high charge density resulting from its six phosphate ester groups.

In water bodies, with few absorbing surfaces and constant mixing, organisms can take up P much more easily than from a soil matrix, where sorption is strong and transport towards uptake surfaces is limited by diffusion. Even low concentrations of P are therefore very effective in increasing the biological productivity of aquatic systems. This makes aquatic systems highly sensitive to P contamination. Phosphate losses from land to water, commonly have significant eutrophying effect on surface waters.

THE BIOLOGICAL IMPORTANCE OF P

Phosphorus is an essential element of biological systems. It is part of the genetic material and the phosphate ester bond is universally used for energy transfer reactions in organisms. Plants take up and concentrate P from near 0.1 mg P L⁻¹ in soil solution to 100 mg P L⁻¹ in xylem sap, and can accumulate near 4,000 mg P kg⁻¹ in seeds. Mammals contain around 25,000 mg P kg⁻¹ dry weight. Because of the importance of P in biological processes, changes in P availability can have major impacts on ecosystem function and structure. Often both N and/or P availabilities may be near limiting levels, but the dependence of biological N fixation on adequate P supply makes P the principal limiting element of ecosystems. The biological importance of P, means that ecosystems have developed mechanisms by which P is taken up, recycled and retained efficiently (Cole et al. 1977; Attiwill and Adams 1993). In dystrophic or oligotrophic tropical forests, a significant portion of P is cycled biologically within the plant biomass, thus it is protected from conversion to soil P of low solubility. Lal et al. (2001) estimated that between 20% to 91% of the P demand of Indian dry forest trees was satisfied by re-translocation of P prior to leaf abscission. The extent of re-translocation reflects soil nutrient availability (Tiessen et al. 1994). Recycling through mineralization of organic P from plant residues also contributes to plant P requirements (Frossard et al. 2000). Annual recycling of P to soil in above- and below-ground plant residues represented 18–38% and 15–80% (mean 55%) of plant P uptake in temperate crop and forest ecosystems, respectively (Hanway and Olsen 1980; Pritchett and Fisher 1987). In dystrophic forests, much of the P uptake by roots may be directly from plant litter via the
hyphae of mycorrhiza. The biological and biochemical processes of P cycling are more important in tropical soils than in most temperate environments, because of the combination of lower inorganic P availability and greater biological activity in the tropics. The high biological potential of the humid tropics is evident in the large biomass production and rapid turnover of organic matter, and also in the very intensive land use. Up to four crops can be planted and harvested per year on a single plot, generating high nutrient demand.

THE AGRICULTURAL IMPORTANCE OF P

Much of tropical agriculture is undercapitalized with respect to P fertility. Mailly et al. (1997) illustrate a P-budget typical for most low input agriculture over a six-year cultivation cycle in Java. Of the 130 kg P ha\(^{-1}\) accumulated in plants during the cycle, half were removed in harvested materials. Fertilization replenished only 45 kg P ha\(^{-1}\). In addition, P stocks of arable fields are frequently depleted further by erosion. In a study on the P fluxes in low input agriculture in northeast Brazil, Menezes and Sampaio (2002) showed the largest P flow was associated with erosion from cultivated fields (6 kg ha\(^{-1}\) year\(^{-1}\)), followed by the erosive flow from (generally overstocked) pastures. By comparison to these erosive flows, the output of P from the farm by crop (2 kg ha\(^{-1}\) year\(^{-1}\)) and animal (0.2 kg ha\(^{-1}\) year\(^{-1}\)) products was minor.

Biological cycling of P is rarely sufficient to supply P to highly productive cropping systems. Continued inputs of P in the form of fertilizers are required to sustain high levels of production after the initial mineralization of soil organic matter, commonly associated with bringing land under cultivation. On North American grasslands, this initial release of P from inherited soil organic matter lasted for some 60 years of cultivation without P inputs, and resulted in 20–30% decreases in soil organic P (Tiessen et al. 1982). Following these first 60 years of cultivation, fertilizer use in the region increased many-fold.

Crop P fertilizer requirement varies with soil type, from <1 kg P ha\(^{-1}\) in relatively unweathered soils of arid environments to 200 or 300 kg P ha\(^{-1}\) in oxide rich tropical or volcanic soils. As a result, oxidic tropical and subtropical soils, which are often in regions with low purchasing power, account for 50% of the world inorganic P fertilizer requirements for crop production. Crop production on such soils without inorganic P fertilisation will degrade the (agro-) ecosystem. The important role of P in maintaining ecosystem quality is demonstrated by the need for large P inputs in restoration strategies that combine P fertilisation with the planting of N-fixing legumes for degraded lands in Southeast Asia. During the plant succession following P application, P is recycled in plant residues, which decompose to release P in quantities and at rates greater than those determined by inorganic P availability. As a result, plants with higher P demand can grow, thus re-creating an organic P supply cycle that can effectively compete with inorganic P sorption and prevent P losses by runoff and leaching. Soil P availability will
remain a major constraint on food production. Management of P fertilizer inputs, together with an understanding of organic matter cycling, should allow for the development of more sustainable agriculture practices.

ECOSYSTEM P AND THE IMPACT OF HUMAN ACTIVITY

The distribution of total ecosystem P between soils and plants varies widely. In a grazed permanent pasture, herbage P amounted to only 1% of the total P content of topsoil (0–20 cm; Williams and Haynes 1992), whereas above- and below-ground plant parts of a temperate forest accounted for 38% of total P in the ecosystem (Hart et al. 2003). In many dystrophic tropical forests, the largest reservoir of nutrient elements is in the plant biomass. In the total (300 t ha⁻¹) aboveground biomass, of a P-limited Colombian tropical rainforest, Rodriguez-Jimenez (1988) measured 40 kg P. Such differences in P contents and elemental ratios reflect plant community adaptation to geochemical constraints.

Elevated P concentrations in the environment are often an indicator of (past) biological or human activity. Megalithic and Khalahari campsites and Terras Pretas do Indio in the Amazon all show a clearly elevated P content. Even the “industrial” fertilizer P, mined from rock phosphate with a P concentration of approximately 150,000 mg kg⁻¹, is ultimately derived from biological processes. It is the product of the sedimentation and accumulation of marine organisms.

Human impacts have substantially altered global P transformations and transfers. Phosphorus transfers in the environment are closely correlated with human occupation, as shown by the regression between P exports from watersheds and their population density: loss rates of 0.3 kg P km⁻² at a population density of 0.1 km⁻², rising to 30 kg P km⁻² at densities of 300 km⁻² (Caraco 1995). In the Canadian province of British Columbia, diatom records in lake sediments show a significant P enrichment since 1850, the time of European settlement. The advent of inorganic P fertilizers and concentrated livestock production in some areas has greatly increased P loads in surface waters (Anderson 1997). Particularly in richer nations, inorganic P fertilizer use and concentrated livestock production have increased P loads and transfers to surface waters. The P balance for a lake watershed in Sweden, a wealthy nation with a sound environmental policy, suggests 62% of P inputs came from inorganic P fertilizer, 30% from manure, 5% from sewage, 2% from atmospheric deposition and 0.3% from the natural weathering of rocks (Ryding et al. 1990). Phosphorus outputs were, 93% in crop exports, 6% in erosion from arable land and 0.6% was leached to ground water. The total P inputs were three times greater than outputs; i.e. the watershed showed a net P accumulation.

The surplus of P in highly developed regions is in stark contrast to the nutrient deficiencies in many developing countries. While P reserves in soils of highly developed agricultural areas are increasing, and even reaching saturation, many tropical soils have a large P deficit, aggravated by high P fixation capacities that reduce fertilizer availability. Increased food demands from old, weathered, often
tropical soils has reduced the fertility of these soils beyond the traditional capacity for regeneration (such as under shifting cultivation) and land degradation is evident. Phosphorus availability in these soils is very low and will not sustain growing populations without extra P inputs.

World trade movements amount to some 10 million tonnes P year\(^{-1}\), with 81\% of trade in fertilizer, rock or phosphoric acid, 15\% in plant and 1\% in livestock commodities (Beaton et al. 1995). Since trade flows are uneven between world regions, these figures imply an important P enrichment in regions with large and wealthy populations, which import both fertilizers and other P-containing commodities. An equalization of P availabilities around the globe would require large resources, investments in effective P recycling and an increased value-added activity in primary producer regions. Shipping livestock products rather than soybean for instance, would avoid some of the nutrient concentration in rich intensive livestock production regions. While the need for efficient use of P has prompted human populations to evolve elaborate management strategies for maintaining P fertility in agriculture, recycling P and limiting P pollution from wastes, improvements in management and shipping patterns are still needed if increasing populations are to manage their environments sustainably.

Regions that import large P surpluses endanger the biological integrity of their surface waters. Although most watersheds will show a net P retention, even with substantial P inputs, they are leaky, and rates of P export are higher after P application than natural levels. Phosphorus inputs into fresh waters can increase growth of algae and aquatic weeds and lead to oxygen shortages due to their decomposition. Remedial action in such cases has focused on the role of P, although N is also essential for the growth of aquatic biota. The focus on P is due to the difficulty in controlling the fixation of atmospheric N by blue-green algae (Sharpley and Rekolainen 1997). Some 10\% of P export from land occurs by leaching and ground water transport, while 90\% is transported by overland flow as sediment or dissolved P. Despite the small proportion of leached P, it has a greater effect on eutrophication of receiving waters because it is soluble and therefore easily available to biota. Phosphorus losses by over-land transport range from 0.1 to 10 kg ha\(^{-1}\) year\(^{-1}\), or more on highly erosive sites.

On average, surface runoff waters carry 10 \(\mu g\) L\(^{-1}\) of dissolved and 1,000 \(\mu g\) L\(^{-1}\) of sediment P (Melak 1995). While P is transported down-stream, sedimentation and re-suspension occur. Phosphorus is released from the sediment when solution P is diminished. The concomitant movement and recycling of P results in a “spiral-ing” of P as it moves down rivers. Inland lakes are affected by past fertilizer and animal waste management. More dialogue between freshwater and land use practitioners on the transfers of nutrients between systems is needed to develop regional plans to prevent P loss.

Globally some 33 million tonnes P year\(^{-1}\) are discharged into oceans, of which, more than half is carried by rivers and the remainder is coastal runoff (Howarth et al. 1995). Most of the input to oceans is ultimately buried in sediments, through processes lasting millions of years. Coastal seas receive both sediment-bound and dissolved P. The bio-available portion of P in fluvial transport is estimated to be
approximately 2 million tonnes P year$^{-1}$ and is responsible for the high productivity of near-shore waters. The sensitivity of coastal regions means that prevention should be favored over damage management. Water of the high oceans contains only 0.01 mg P L$^{-1}$, and P is critically limiting productivity of these waters.

One problem with quantifying the role of P in the global environment is the difficulty in measuring the biologically active or available portion of P. Phosphate availability is a function of chemical equilibrium-controlled solubilities and sorption reactions, and of rate-limited biological processes. Most methods for determining available P attempt to quantify only the chemical solubility of P using different extractants, but few relate this to P supply rates to plants. Soil test methods extract a portion of soil P that is related to plant available P, as estimated by regression equations established over years of agronomic experimentation and testing of fertilizer responses. Results obtained with this approach are rarely transferable between crops or soil types. The approach does not work at all when perennial plants or natural ecosystems are examined, because measurable pools are often small, and biological P re-cycling determines P availability. Since available P is constantly replenished, it is strongly time dependent. This makes available P a functional concept rather than a measurable quantity.

REFERENCES

Chapter 2
CARBON/NITROGEN/PHOSPHORUS ALLOMETRIC RELATIONS ACROSS SPECIES

Karl J. Niklas

INTRODUCTION

This chapter reviews some of the ecological and evolutionary implications of carbon (C), nitrogen (N), and phosphorus (P) stoichiometry and the allometric relationships among these elements reported for terrestrial plant species because the patterns of C mass allocation and N:P-stoichiometry for different plant organ-types are of general interest to understanding a broad range of ecological and evolutionary phenomena (Aerts and Chapin 2000; Bazzaz and Grace 1997; Chapin et al. 1986; Grime 1979; Niklas and Enquist 2001, 2002; Westoby et al. 2002; Wright et al. 2004; Niklas et al. 2005, 2007; Kerkhoff et al. 2006). Much of the functional-trait variation observed among species differing in overall size can be attributed to differences in the amount of C, N or P allocated to the construction of leaves, stems, roots, and reproductive structures as well as to differences in overall body size (Grime 1979; Field and Mooney 1986; Tilman 1988; Bazzaz and Grace 1997; Jackson et al. 1997; Milberg and Lamont 1997; Weiher et al. 1999; Niklas and Enquist 2001, 2002; Enquist and Niklas 2002; Westoby et al. 2002; Wright et al. 2004; Niklas et al. 2005, 2007; Kerkhoff et al. 2006). Likewise, the P and N concentrations in plant tissues critically influence the material and energy cycles of whole ecosystems (Chapin et al. 1997; De Angelis 1980; Kerkhoff et al. 2005; Koerselman and Meuleman 1996; Silver 1994; Sterner and Elser 2002; Vitousek 1982; Vogt et al. 1986; Ågren and Bosatta 1996) and phylogenetic functional trait differences in the ability to acquire and use N or P are temperature-dependent, such that climatic shifts of sufficient magnitude (e.g., along latitudinal or altitudinal gradients) can have major affects on the C economy of terrestrial vegetation (Kerkhoff et al. 2005; Wright et al. 2005; Westoby and Wright 2006).

The allocation of N and P to leaves is of particular interest because leaves provide the principal means by which vascular plants capture sunlight. Both N and P play pivotal roles in photosynthesis and respiration, and their abundance also influences the consumption of leaves by herbivores (Cebrian 1999; Elser et al. 2000a,b; Mattson 1980). In addition, the availability of N and P is known to limit the growth of both terrestrial (Chapin et al. 1986; Ågren 1988; Güsewell 2004) and aquatic plants (e.g. Klausmeier et al. 2004; Karpinets et al. 2006). Further, coordinated patterns of variation in N and P have been observed across the leaves...
of phylogenetically and ecologically unrelated plant species. These patterns have received particular attention in the light of recent stoichiometric models that draw attention to the biochemical constraints imposed on plant growth by the allocation of N to tissue proteins (which are particularly N-rich) and the allocation of P to the ribosomal RNA “machinery” used to synthesize proteins (Sterner and Elser 2002; Ågren 2004; Güsewell 2004; Wright et al. 2004; Kerkhoff et al. 2005; Niklas and Cobb 2005; Niklas et al. 2005, 2006, 2007).

QUARTER-POWER SCALING “RULES” AND N:P-STOICHIOMETRY

Stoichiometric models are especially relevant to theories purporting to explain the apparent ubiquity of quarter-power scaling “laws” that span all levels of biological organization, from molecules to ecosystems, across prokaryotes and eukaryotes, and among plants and animals (Hemmingsen 1960; Peters 1983; Calder 1984, 1996; Schmidt-Nielsen 1984). For example, across animal species ranging in size from that of a mouse to an elephant, maximum life span in captivity, blood volume circulation, fast muscle contraction, and a host of other phenomena each scale closely to the 1/4 power of body mass (Lindstedt and Calder 1981). Perhaps the most famous of these rules is Kleiber’s, which states that basal metabolic rates scale as the 3/4 power of body mass (Kleiber 1932, 1961) – a scaling relationship that finds its analog in the allometry of growth rate versus body mass across the polyphyletically and ecologically diverse unicellular algae and terrestrial plants (Banse 1976; Niklas 1994; Niklas and Enquist 2001).

Yet, the identification of an unambiguous mechanistic explanation for the origin of these scaling rules remains an open theoretical problem. Numerous theories have been advanced, but each has been viewed with considerable skepticism (e.g. Blaxter 1965; Blum 1977; Gray 1981; Heusner 1982; Feldman 1995; Economos 1982, 1983; Prothero 1986a). Among the most recent of these, is the theory of Geoffrey B. West, James H. Brown and Brian J. Enquist (denoted hereafter as the WBE theory) who assert that all quarter-power scaling rules (and their 1/4 multiples like 3/4) emerge from the interplay among the physical or geometric constraints resulting from three functional properties of every biological system (West et al. 1997, 1999, 2001). Specifically, their theory claims that for biological systems, all networks (1) are space-filling, hierarchical branching systems, (2) have terminal branch elements that are invariant in size, and (3) by virtue of natural selection, minimize the energy required to transport and deliver nutrients (and thus minimize either the time or distance nutrients are moved).

As so many theories before it, the WBE theory has been heavily criticized on empirical, theoretical, and even strictly mathematical grounds (e.g. Dodds et al. 2001; Darveau et al. 2002; Weibel 2002). Arguably, the first assumption (i.e. that biological delivery networks are “fractal” in nature) is consistent with the “self-similarity” typically observed when branched nutrient networks within
multicellular organisms are dissected and numerically quantified. However, if the WBE theory is valid across all levels of biological organization, from that of molecules to ecosystems as claimed by its authors, fractal-like delivery networks must exist at each level, which is difficult to imagine for some levels of biological organization (e.g. molecules) and undocumented for others (e.g. organelles and ecosystems). Similar concerns exist for the two remaining assumptions of the WBE theory. It has yet to be established that capillaries, bronchioles, and terminal xylary elements are invariant in size or that they minimize the time and energy required to exchange mass or energy.

Despite these concerns (or perhaps because of them), the WBE theory has engendered a renaissance in the field of allometric theory and empirical enquiry – one in which alternative theories for the existence of quarter-power scaling rules continue to be sought. It is in this context that recent developments in modeling the effects of N and P allocation patterns on protein synthesis rates (and thus “growth”) are particularly exciting. These models emerge from the perspective that, irrespective of phyletic affinity or ecological preference, the growth rate of any kind of organism is positively correlated with ribosome number and rate of activity and negatively correlated with protein concentration (Dobberfuhl 1999; Sterner and Elser 2002; Elser et al. 2003; Ågren 2004; Vrede et al. 2004). Conceptually, the amounts of ribosomes and proteins are thought of as respective measures of an organism’s protein-production “machinery” and the “overhead” that must be produced per unit time to maintain a constant growth rate. N:P-stoichiometry is emphasized, because large fractions of an organism’s N and P are allocated to the construction of proteins and rRNA, respectively. Thus, N:P-stoichiometry is predicted to correlate with growth rate at the level of cells, tissues and the whole organism (Dobberfuhl 1999; Sterner and Elser 2002; Vrede et al. 2004). Specifically, growth rates should correlate positively with increasing rRNA (and P) investments relative to protein (and N) investments.

This prediction is particularly relevant to three previously reported allometric relationships for plants (Niklas and Enquist 2001, 2002). First, annual growth rates in body mass across phyletically and ecologically diverse species appear to scale as the 3/4 power of body size. Second, growth rates scale linearly (isometrically) with the capacity to intercept sunlight. Third, total leaf N appears to scale as the 3/4 power of total leaf P, across and within some species (Niklas and Cobb 2005; Niklas et al. 2005, 2007). The goal of this paper is to review these relationships and to explore them empirically with the aid of a recently expanded database for nonwoody and woody plant species ranging across eleven orders of magnitude in total body size.

A STATISTICAL ASIDE

Biological scaling relationships, referred to as “power rules”, comply mathematically with the formula

\[ Y_\alpha = \beta Y_\alpha^\alpha \]
where \( Y_o \) and \( Y_a \) are the variables plotted on the ordinate and abscissa axes, respectively, \( \beta \) is the normalization constant, and \( \alpha \) is the scaling exponent. In most, but not all cases, \( Y_a \) is some measure of mass (typically, but not invariably, expressed in units of carbon mass). When \( \alpha = 1 \), the formula \( Y_o = \beta Y_a \) describes an isometric relationship that plots as a straight line on both linear and logarithmic axes. When \( \alpha \neq 1 \), the formula \( Y_o = \beta Y_a^\alpha \) describes an allometric relationship that plots as a linear function on logarithmic axes. Logarithmic transformation shows that \( \log \beta \) and \( \alpha \) are the \( Y_o \)-intercept (“elevation”) and the slope (“scaling exponent”) of the log-log linear allometric relationship, respectively, i.e.

\[
\log Y_o = \log \beta + \alpha \log Y_a
\]

The linearization of data by means of logarithmic transformation has become a conventional practice in allometric studies, in part because it minimizes the sum of squared residuals for the transformed as opposed to the original function. It should be noted, however, that regression parameters estimated in this way do not invariably provide the best fit of data to a regression model compared to minimizing the squared residuals for the actual function by using nonlinear regression protocols. Analyses of residuals are required to determine whether log-log linear or log-log nonlinear functions optimize the goodness of fit. This protocol does not appear to be a “standard practice”, perhaps because most allometric theories assert (or insist on) the existence of numerically unique scaling exponents, which do not exist for log-log nonlinear relationships.

The objective of the vast majority of allometric studies is to determine the numerical values of \( \log \beta \) and \( \alpha \). When a predictive relationship is sought, simple ordinary least squares regression (OLS) analysis can be used. When the objective is to establish a functional relationship between \( Y_o \) and \( Y_a \), as is generally the case, OLS regression analysis is ill equipped for this purpose, in part because it is based on the assumption that \( Y_a \) is biologically independent of \( Y_o \) and that it is measured without error. Three regression methods have been suggested to overcome this limitation, i.e. Bartlett’s three-group method, principal axis regression, and reduced major axis regression (Sokal and Rohlf 1980), which has been recently renamed as standardized major axis regression (Warton et al. 2006). Considerable controversy revolves around which of these methods is the most appropriate (Smith 1980; Harvey 1982; Prothero 1986b; Seim 1983; Rayner 1985; McArdle 1988, 2003; Jolicoeur 1990; Warton et al. 2006). This issue is not trivial, especially when the goal is to “test” when empirically determined scaling exponents agree statistically with those predicted by a particular theory, because the numerical values of \( \alpha \) and \( \log \beta \) depend on the regression techniques used and because different techniques can produce significantly different numerical values even for the same data set.

Space precludes a detailed discussion of the merits and detractions of each of the three regression methods. However, standardized major axis (SMA) regression analysis has emerged as a “standard” allometric technique over the past few years. Statistical software is available to perform SMA regression analyses, but access to
this software is not critical, because OLS regression summary statistics provide all the necessary information to compute the numerical values of $\alpha$ and $\log \beta$, and their corresponding 95% confidence intervals.

Specifically, these regression parameters can be computed using the formulas

$$\alpha_{SMA} = \frac{\alpha_{OLS}}{r}$$

and

$$\log \beta_{SMA} = \log \bar{Y}_a - \alpha_{RMA} \log \bar{Y}_a,$$

where $\alpha_{SMA}$ is the (reduced major axis) scaling exponent, $\alpha_{OLS}$ is the OLS regression slope, $r$ is the OLS correlation coefficient, $\log \beta_{SMA}$ is now called the allometric constant, and $\log \bar{Y}$ denotes the mean value of $\log Y$. The corresponding 95% confidence intervals of these two regression parameters are computed using the formulas

$$\alpha_{SMA} \pm t_{N-2} \left( \frac{MSE}{SS_a} \right)^{1/2}$$

and

$$\log \beta_{SMA} \pm t_{N-2} \left[ MSE \left( \frac{1}{N} + \frac{\log Y_a^2}{SS_a} \right) \right]^{1/2},$$

where $MSE$ is the OLS mean square error, $SS_a$ is the OLS sums of squares for $\log Y_a$, $N$ is the sample size, and $t_{N-2} = 1.96$ when $N - 2 > 120$.

**LIGHT, GROWTH, AND BODY SIZE**

Two scaling relationships appear to cut across phyletically diverse unicellular algae and tree-sized embryophytes (Banse 1976; Niklas 1994, 2004; Niklas and Enquist 2001). Growth in dry C mass per individual per year ("annual growth", $G_T$) scales isometrically with respect to the capacity to intercept sunlight (quantified by pigment concentration per cell for unicellular algae, $C_p$, and by standing leaf mass for tree species, $M_L$), and annual growth scales as the 3/4 power of body mass (total cell or organism dry mass, $M_T$). Respectively, these scaling relationships are expressed by the isometric and allometric formulas

$$H = \beta_0 G_T,$$
and

\[ G_T = \beta_1 M_T^{3/4}, \]

where \( H \) denotes \( C_P \) or \( M_L \) and allometric constants are distinguished from each other by different numerical subscripts. Combining these two scaling relationships leads to the prediction that the ability to harvest sunlight as gauged by \( C_P \) or \( M_L \) is proportional to the 3/4 power of total body mass, i.e.

\[ H = \beta_2 M_T^{3/4}, \]

where \( \beta_2 = \beta_0 \beta_1 \). These log-log linear scaling relationships are illustrated in Figures 2.1 and 2.2.

An isometric relationship between \( H \) and \( G_T \) makes intuitive sense. Even though the ability to “harvest sunlight” and its corresponding “energy use efficiency” are very different biophysical phenomena, it is not unreasonable to expect growth rates to correlate linearly with the ability to capture radiant energy. In contrast, it is not obvious why either annual growth rate or light-harvesting ability should scale as the 3/4 power of body mass. Early workers exploring the relationship between basal metabolic rates across animals differing in body size expected a 2/3 scaling exponent, because they assumed that the ability of cells or entire organisms to exchange mass or energy with the environment is dictated by body surface area (which scales

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**Fig. 2.1** Bivariate relationship between log10-transformed data for annual growth in total dry mass per plant \( (G_T) \) and total body mass \( (M_T) \) for unicellular algae, herbaceous species, and trees (see insert for key to symbols). Original units: \( G_T = \) pg C per cell per day (algae) and kilogram dry mass per embryophyte per year; \( M_T = \) pg C per algal cell (algae) and kilogram dry mass (embryophytes). Solid line, standardized major axis regression curve (for all data); see Table 2.1 for regression statistical summary. (Data from Niklas and Enquist 2001.)
as the square of any linear reference dimension \( L \) and that the demand for nutrients is correlated with body volume (which scales as the cube of \( L \)). Importantly, the 2/3 scaling relationship between surface area and volume holds true only for a series of geometrically identical objects that retain the same shape as they increase in size – two conditions that are repeatedly violated by unicellular and multicellular organisms, both ontogenetically and phylogenetically.

Regardless of the mechanistic explanation for why the three scaling relationships exist, each receives reasonably strong statistical support when “tested” against empirically observed trends for phylogenetically diverse unicellular algae and tree-sized dicots and conifers (Table 2.1). For these organisms, the 95% confidence intervals of the slope of the log-log linear relationship between light harvesting capability and annual growth approach or include unity. Likewise, the intervals of the slope of the log-log linear relationship between annual growth and total body mass include 0.75. Thus, the proportional relationships summarized by \( H \propto G_T \propto M_T^{3/4} \) are reasonably accurate across unicellular algae and tree-sized plants.

In pointed contrast, the allometry of nonwoody plants (i.e. herbaceous species and one-year old dicot and conifer tree species) deviates from these predictions, because it is strongly isometric in terms of all three biological variables, i.e., \( H \propto G_T \propto M_T \) (Table 2.1). Consequently, the 3/4 scaling “rule” is neither “invariant” nor “universal”.

**Fig. 2.2** Bivariate relationship between log_{10}-transformed data for total light-harvesting capacity \( (H) \) and annual growth in total dry mass per plant \( (G_T) \) and total body mass \( (M_T) \) for unicellular algae, herbaceous species, and trees (see insert for key to symbols). Original units: \( H = \) pg photosynthetic pigments per cell per day (algae) and kilogram dry leaf mass per plant per year; \( G_T = \) pg C per cell per day (algae) and kilogram dry mass per embryophyte per year. Solid line, standardized major axis regression curve (for all data); see Table 2.1 for regression statistical summary. (Data from Niklas and Enquist 2001.)
That growth does not invariably scale as the 3/4 power of body mass is evident from the analyses of data for nonwoody vascular plants presented in the previous section. However, the claim that annual growth across ecologically and phyletically diverse unicellular and multicellular photoautotrophic eukaryotes scales isometrically or nearly so with respect to light harvesting ability (see Niklas and Enquist 2001, 2002) is statistically robust (Table 2.1). In the case of unicellular photoautotrophs, \( H \) is measured in units of photosynthetic pigment concentrations per cell, \( C_p \). However, for terrestrial embryophytes, \( H \) is measured in terms of standing dry leaf mass per plant, \( M_L \). Thus, annual growth appears to be inexorably linked to the “machinery” of photosynthesis in some very basic way that cuts across otherwise sharply defined phyletic boundaries.

This linkage probably exists at numerous metabolic and structural levels, but the view advocated here is that it is sensitive to the manner in which N and P is allocated in light harvesting structures (e.g. moss phyllids, “microphylls” and “euphyls”, and entire tree canopies). This perspective is based on the comparatively strong scaling relationships that exist between total leaf carbon mass (\( M_{C} \)) and total leaf N and P (\( M_N \) and \( M_P \), respectively) – relationships that appear to obey their own quarter-power “rules” across and within those species that have been examined in sufficient detail.

For example, based on stoichiometric data collected from 131 herbaceous species, including \( C_3 \) and \( C_4 \) species, Niklas et al. (2005) report that leaf N content scales almost isometrically with respect to increasing leaf carbon content, whereas leaf P content scales as the 4/3 power of leaf carbon content (Figure 2.3a; Table 2.2).
For these species, it follows from $M_N \propto M_C$ and $M_P \propto M_C^{4/3}$ such that $M_N \propto M_P^{3/4}$, which should also hold true for N and P content expressed as percentages (Figure 2.3b; Table 2.2). Although stoichiometric analyses of plant conspecifics differing in size are sparse, the data that are available indicate that intraspecific trends may abide by the same “rules”. For example, in a study of *Eranthis hyemalis* (a perennial member of the Ranunculaceae), Niklas and Cobb (2005) report scaling exponents

![Bivariate relationships among log10-transformed data for total leaf nitrogen, phosphorus, and carbon content ($M_N$, $M_P$, and $M_C$, respectively) and percentage of leaf nitrogen and phosphorus content.](image-url)

**Fig. 2.3** Bivariate relationships among log10-transformed data for total leaf nitrogen, phosphorus, and carbon content ($M_N$, $M_P$, and $M_C$, respectively) and percentage of leaf nitrogen and phosphorus content. a. $M_N$ and $M_P$ versus $M_C$ for 131 species. (Data from Niklas et al. 2005.) b. % $M_N$ versus % $M_P$ for 131 species. (Data from Niklas et al. 2005.) c. % $M_N$ versus % $M_P$ for 7,445 species. (Data from Reich and Oleksyn 2005.) Original units: gram mass per leaf gram dry mass. Solid lines, standardized major axis regression curves; see Table 2.2 for regression statistical summaries
Fig. 2.4  Bivariate relationships among log_{10}-transformed data for nitrogen, phosphorus, and carbon content (\( M_N \), \( M_P \), and \( M_C \), respectively) for organs and plant parts of *Eranthis hyemalis* (see insert for key to symbols: \( R \) = roots, \( AS \) = aerial stems, \( L \) = leaves, \( F \) = developing fruits and seeds, \( US \) = tubers from growing plants; \( US' \) = tubers from winterized plants). See Table 2.2 for regression statistical summaries. (Data from Niklas and Cobb 2005.)

![Graph](image)

**Table 2.2** Standardized major axis regression scaling exponents, allometric constants, and their respective 95% confidence intervals for log_{10}-transformed data of total leaf nitrogen, phosphorus, and carbon content (\( M_N \), \( M_P \), and \( M_C \), respectively)

<table>
<thead>
<tr>
<th></th>
<th>( \alpha_{SMA} ) (95% CI)</th>
<th>( \log \beta_{SMA} ) (95% CI)</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Across herbaceous species (n = 131)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \log M_N ) vs. ( \log M_C )</td>
<td>1.06 (0.95; 1.17)</td>
<td>−1.67 (−1.76; −1.58)</td>
<td>0.941</td>
</tr>
<tr>
<td>( \log M_P ) vs. ( \log M_C )</td>
<td>1.37 (1.27; 1.48)</td>
<td>−2.61 (−2.70; −2.52)</td>
<td>0.968</td>
</tr>
<tr>
<td>( \log M_N ) vs. ( \log M_P )</td>
<td>0.78 (0.72; 0.85)</td>
<td>−0.74 (−0.72; −0.76)</td>
<td>0.948</td>
</tr>
</tbody>
</table>

*Eranthis hyemalis* (n = 17)

<table>
<thead>
<tr>
<th></th>
<th>( \alpha_{SMA} ) (95% CI)</th>
<th>( \log \beta_{SMA} ) (95% CI)</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \log M_N ) vs. ( \log M_C )</td>
<td>1.00 (0.98; 1.03)</td>
<td>−1.33 (−1.39; −1.26)</td>
<td>0.996</td>
</tr>
<tr>
<td>( \log M_P ) vs. ( \log M_C )</td>
<td>1.37 (1.32; 1.42)</td>
<td>0.77 (0.65; 0.90)</td>
<td>0.993</td>
</tr>
<tr>
<td>( \log M_N ) vs. ( \log M_P )</td>
<td>0.73 (0.70; 0.76)</td>
<td>−1.89 (−1.97; −1.82)</td>
<td>0.996</td>
</tr>
</tbody>
</table>

Across Reich and Oleksyn (2004) data set (n = 7,445)

<table>
<thead>
<tr>
<th></th>
<th>( \alpha_{SMA} ) (95% CI)</th>
<th>( \log \beta_{SMA} ) (95% CI)</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \log M_N ) vs. ( \log M_P )</td>
<td>0.73 (0.71; 0.75)</td>
<td>1.08 (1.07; 1.08)</td>
<td>0.33</td>
</tr>
</tbody>
</table>
for $M_N$, $M_P$ and $M_C$ relationships that are statistically indistinguishable from the proportional relationships $M_N \propto M_C$ and $M_P \propto M_C^{4/3}$ and $M_N \propto M_P^{3/4}$ even at the level of organ-type (Table 2.2; Figure 2.4).

Whether these scaling relationships are “universal” properties of vascular plant biology remains problematic. Based on an extensive world-wide survey of leaf N and P composition, Wright et al. (2004) reported that leaf N content scales roughly as the 2/3 power of leaf P content. In contrast, using an expanded version of the leaf N and P data reported by Reich and Oleksyn (2004) consisting of 7,445 entries for individual species reflecting conspecifics differing in age, regression analysis of $M_N$ versus $M_P$ reveals a scaling exponent of 0.73 with 95% confidence intervals that include the numerical value of 3/4 but exclude that of 2/3 (Figure 2.3c; Table 2.2).

This inconsistency may be the result of phyletic effects (i.e. biases introduced by differences in the taxonomic composition of the data sets used). However, regardless of the reason, it is clear that the relationship between leaf N and P content is allometric and governed by the generic formula

$$M_N = \beta M_P^{<1.0}$$

### N:P-STOICHIOMETRY AND GROWTH MODELS

This “generic” formula has added significance when it is juxtaposed with stoichiometric models for predicting relative growth rates based on cell or tissue N and P content. Dobberfuhl (1999) first proposed that growth depends on total body N ($N_T$) and total body P ($P_T$) allocation to protein and ribosomal RNA (also see Sterner and Elser 2002; Ågren 2004; Vrede et al. 2004). This model conceptually relates relative growth rates to N:P-stoichiometry by envisioning proteins as the “overhead” required to achieve growth and rRNA as the protein-output “machinery” used to maintain or recycle this overhead. Dobberfuhl and others noted that, when an organism maintains a constant chemical composition, its relative growth rate $\mu$ can be mathematically expressed in terms of the amounts and rates of change of carbon (C), nitrogen (N), and phosphorus (P) content by the formula

$$\mu = \frac{1}{C} \left( \frac{dC}{dt} \right) = \frac{1}{N} \left( \frac{dN}{dt} \right) = \frac{1}{P} \left( \frac{dP}{dt} \right).$$

For any one of these essential substances, designated as $X$, $\mu$ can be approximated by the formulas

$$\mu = \frac{1}{X} \left( \frac{dX}{dt} \right) = \ln \left( \frac{X_2}{X_1} \right) \cdot (t_2 - t_1)^{-1},$$
where $X_2$ is the total concentration of substance $X$ at time $t_2$ and $X_1$ is the total concentration of $X$ at time $t_1$ (see Hunt 1990). If $X$ is some measure of protein synthesis, the formulas for $\mu$ can be recast as

$$\mu = \ln \left[ \frac{f_N N_T + \left( \frac{k_s r F f_P P_T}{m_r} \right)}{f_N N_T} \right] t^{-1},$$

where $f_N$ is the decimal fraction of $N_T$ invested in proteins, $k_s$ is the protein synthesis rate per ribosome, $r$ is the protein retention efficiency, $F$ is the decimal fraction of total RNA allocated to rRNA, $f_P$ is the decimal fraction of $P_T$ invested in RNA, $m_r$ is the mass of an average ribosome, and $t$ now denotes the time interval $t_2 - t_1$ (Dobberfuhl 1999; Vrede et al. 2004).

The relative growth rates of very different unicellular algae and small aquatic animals have been successfully predicted using this approach or ones similar to it (e.g. Nielsen et al. 1996; Klausmeier et al. 2004; Vrede et al. 2004) despite the assumptions that $N_T$ and $P_T$ allocation patterns are ontogenetically invariant, that balanced growth has been achieved, and the supposition that resources are not limiting. In addition, this approach has been integrated with allometric theory by noting that the ability to harvest light scales isometrically with respect to total annual plant growth across unicellular algae and vascular plant species (Table 2.1; Niklas and Enquist 2001).

As noted for vascular plants, this ability is gauged by standing leaf dry mass $M_L$. Consequently, the relative growth rate of leaves $\mu_L$ may provide a reliable gauge of the relative growth rate of the entire plant body. Accordingly, if the formula for $\mu$ is generally valid, $\mu_L$ should be governed by total leaf $N$ and $P$ such that

$$\mu_L = \ln \left[ 1 + \left( \frac{k_s r F}{m_r} \right) \left( \frac{f_P}{f_N} \right) \frac{M_P}{M_N} \right] t^{-1}.$$

Combining this relationship with the observation that $M_N = \beta_3 M_P^\alpha$ obtains a quantitative description of leaf relative growth rates in terms of the allometry of total leaf $N$ and $P$:

$$\mu_L = \ln \left[ 1 + \left( \frac{k_s r F}{m_r} \right) \left( \frac{f_P}{f_N} \right) \left( \frac{M_P^{\frac{1}{\alpha}}}{M_N^{\frac{1}{\alpha}}} \right) \right] t^{-1}.$$

Note that this formula predicts that leaf relative growth rates will increase across species with either increasing leaf $N$ or $P$ allocations when $\alpha < 1.0$ (see Niklas et al. 2005).