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REVIEW ARTICLE

Phytic acid in green leaves

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ABSTRACT

Phytic acid or phytate, the free-acid form of myo-inositolhexakiphosphate, is abundant in many seeds and fruits, where it represents the major storage form of phosphorus. Although also known from other plant tissues, available reports on the occurrence of phytic acid, *e.g.* in leaves, have never been compiled, nor have they been critically reviewed. We found 45 published studies with information on phytic acid content in leaves. Phytic acid was almost always detected when studies specifically tried to detect it, and accounted for up to 98% of total P. However, we argue that such extreme values, which rival findings from storage organs, are dubious and probably result from measurement errors. Excluding these high values from further quantitative analysis, foliar phytic acid-P averaged 2.3 $mg \cdot g^{-1}$, and represented, on average, 7.6% of total P. Remarkably, the ratio of phytic acid-P to total P did not increase with total P, we even detected a negative correlation of the two variables within one species, *Manihot esculenta*. This enigmatic finding warrants further attention.

INTRODUCTION

Phytic acid or phytate, the free-acid form of myo-inositolhexakiphosphate (InsP6), is found widely in eukaryotes. In plants, phytic acid has been identified as the major storage form of phosphorus (P), but other metabolic functions have also been proposed or demonstrated, *e.g.* the storage of other mineral elements such as K, Mg or Ca, RNA transport or DNA metabolism (review in Raboy 2003). A defensive function against insect herbivores has also been suggested (Green *et al.* 2001). At low concentrations, phytic acid (InsP6) and other inositol phosphates such as InsP4 and InsP5 are arguably ubiquitously involved in cellular signal transduction and regulation in eukaryotic cells (Lee *et al.* 2007; Nagy *et al.* 2009). However, the primary interest in phytic acid is related to the fact that this compound represents a major proportion, typically 60–80%, of total P in mature seeds, which impacts the nutritional quality of this foodstuff both for humans and for livestock. Non-ruminant animals cannot utilise phytic acid because they have no or limited phytase activity in their digestive tract. This reduces the amount of usable P, contributes to water pollution from animal manure and even leads to mineral deficiencies because phytic acid is a powerful chelator for Fe, Mg or Ca. This direct and indirect relevance for human well-being has led to an impressively large body of literature on phytic acid in seeds and fruits (Greenwood *et al.* 1984; Batten & Wardlaw 1987; Lott *et al.* 2000; Bohn *et al.* 2008; Raboy 2009), and considerable effort goes into the breeding low phytic acid crops (Raboy 2009) or crops that produce a heterologous phytase (Brinch-Pedersen *et al.* 2002).

Although it is well established that phytic acid can also be found in other plant organs, such as roots (Campbell *et al.* 1991), tubers (Samotus & Schwimmer 1962) or leaves (Bentsink *et al.* 2003), it was established rather early (*e.g.* de Turk 1933) that phytic acid levels are generally rather low in green foliage. Indeed, influential reviews such as that of Raboy (2003) on the occurrence of this compound in plants do not even mention the occurrence of phytic acid in leaves (only in the special case of duckweeds; Roberts & Loewus 1968), while others (*e.g.* Bieleski 1973) acknowledge in passing that small amounts of phytic acid can be found in green tissue, but the lack of further discussion also suggests the last author's rating of this finding as relatively irrelevant.

Recently, Winkler & Zotz (2009) studied the uptake and allocation of P in epiphytic bromeliads. In these plants, a large proportion of the newly acquired nutrient was not used for immediate growth, but rather stored in green leaves in the form of phytic acid, which accounted for >20% of total P (U. Winkler, unpublished results). These plants typically live in nutrient-poor environments with low and intermittent supply of water and nutrients and are probably primarily limited by low P supply (Wanek & Zotz 2011). Hence, high levels of stored P indicative of luxury consumption did not come as a complete surprise (Chapin 1980), but the storage organs, *i.e.* leaves, seemed remarkable considering the general view of phytic acid in leaves outlined above.

This paper explores the question of how high such exceptional phytic acid concentrations in green leaves really are. We are not aware of either a simple compilation let alone a critical examination of existing data. Hence, we performed a thorough survey of the literature for values of phytic acid in green leaves to allow such an evaluation. Apart from scattered reports on the role of phytic acid in herbivore deterrence (*e.g.* Green *et al.* 2001), the study from Winkler & Zotz (2009) was one of the first to indicate a potentially important ecological role of phytic acid in leaves. Considering the prevailing notion that the occurrence of phytic acid in leaves is negligible, it is not surprising that we found few data on phytic acid in leaves from wild plants. Most determinations of phytic acid levels in leaves obtained from the literature were done with plants that are important as leafy vegetables for human consumption (*e.g.* Aletor & Adebayo 2012; Aregheore 2012), used for medicinal purposes (*e.g.* Oboh 2006; Abulude 2007) or as fodder for livestock (*e.g.* Agbede 2005; Kayode & Esiet 2007). There is also a substantial geographical bias: most studies were performed in developing countries, primarily in Africa and Asia, where concerns about the nutritional quality of plant material are most prevalent.

MATERIAL AND METHODS

The basis for this review is a detailed search in a range of Internet databases (among others Web of Science, Google Scholar, World-food.net, Academic search, NCBI, Research gate) for publications on phytic acid concentrations in leaves. We only accepted data that were unambiguously obtained for leaves, analyses of entire shoots were not considered even in *e.g.* grasses because of a possible, yet unknown, contribution of stems and reproductive organs (*e.g.* Onyeonagu *et al.* 2013). This search yielded 45 publications that provided data for phytic acid or phytic acid-P. Only a subset, *i.e.* 17 papers (37%), also supplied information on total P. When not given in the original publication, we calculated phytic acid-P by dividing the amount of phytic acid by 3.55. The resulting data sets represented, respectively, 75 and 35 plant species. Before conducting further analyses, we screened the data of all papers for plausibility as described below.

Typically, values for total P in leaves are around 2 mg·g^{-1} (Schachtman *et al.* 1998), but these vary considerably depending on species and growth conditions (Lambers *et al.* 2008). After careful examination, we discarded four studies with total P < 0.2 mg·g^{-1} because even plants from extremely low-P sites, like *Banksia serrata* attenuata in SW Australia, have leaf P concentrations around 0.2 mg·g^{-1} (de Campos *et al.* 2013). Considering that almost all studied plant species are crops, similarly low values are probably due to measurement errors.

We also excluded those papers in which phytic acid-P exceeded total P. There were two other publications that reported theoretically possible, but highly unlikely, phytic acid-P levels (Abulude 2007; Kayode & Esiet 2007). For example, Abulude (2007) reports results of a survey of leaves of 28 tropical tree species, in which phytic acid represented 36–98% of total P. A histogram of all published phytic acid-P values was bimodal, the second peak being caused exclusively by these two studies (not shown). In all other studies, phytic acid-P was mostly below 10% with a maximum of 25%, while the minimum value reported in these two papers was 36%, the average exceeding 50%, which led to their exclusion.

A final round of revisions and exclusions was based on intraspecific comparisons. Four studies reported low, yet not completely impossible concentrations, *e.g.* 0.03% total P for *Amaranthus hybridus* (Aletor & Adebayo 2012). Since these values were almost two orders of magnitude lower than the results of other studies with the same species (Aletor & Adeogun 1995), these were also excluded from our quantitative analysis.

With the exception of those studies reporting impossible results (phytic acid-P > total P), all studies are listed in Appendix S1, irrespective of their inclusion in the following analyses or not. When necessary, data were log-transformed before performing statistical analyses to satisfy assumptions of normality and homoscedasticity. All tests were run in R (version 2.15.0; R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

This analysis is based on 161 values for phytic acid-P in leaves of 75 species, while 68 values were available both for phytic acid/phytic acid P and total P of the same leaves, representing 35 species. The individual data are shown in Appendix S1, Appendix S2 gives average values of all those species with data on both phytic acid/phytic acid-P and total *P*-values.

With very few exceptions (*e.g.* some subpopulations in Zhao *et al.* 2007), phytic acid was always detected when specifically searched for in analytical studies. The amount of phytic acid-P ranged from zero to 0.004–28 mg·g^{-1} following a log-normal distribution (n = 161; Fig. 1). The average amount of phytic acid-P was 2.3 mg·g^{-1}, but the median was considerably lower (0.5 mg·g^{-1}). Phosphorus concentrations varied from 0.3 to 29 mg·g^{-1}. Phosphorus in phytic acid accounted for 1–27% of total P (Fig. 1), with an average of 7.6% and a median of 5.2%. Remarkably, the proportion of P in phytic acid did not increase with total P; it rather tended to decrease, although not

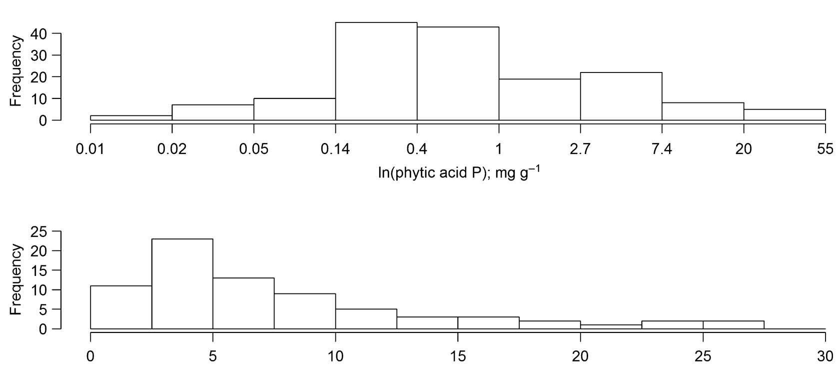

Fig. 1. Histogram of absolute and relative (compared to total P) concentrations of phytic acid-P in leaves. For details see Appendix S1. Upper panel: concentrations of phytic acid-P in mg·g^{-1} of 161 leaf samples from 75 species. Note the logarithmic *x*-axis (natural logarithm). Lower panel: phytic acid-P (as percentage of total P) in leaves. Data represent 35 species.

significantly (Fig. 2; log (phytic acid-P) = −0.3 log (total P) + 1.0; Pearson product moment correlation, $P = 0.16$) for the 35 species. In the only species with a sufficient number of studies, *Manihot esculenta*, for which seven independent data pairs were available, a similar correlation analysis even yielded a highly significant negative result (Fig. 3; log (phytic acid-P) = −0.9 log (total P) + 1.57; Pearson product moment correlation, $r^2 = 0.73$, $P < 0.01$, n = 7).

DISCUSSION

It is well established that phytic acid typically accounts for 60–80% of total P in cereals and 25–90% of total P in other seeds and fruit (Lott *et al.* 2000). Although there are a few publications reporting similarly high values for leaves (*e.g.* Abulude 2007), the validity of such extreme values seems highly questionable. Obviously, including or excluding this and the other study (Kayode & Esiet 2007) with ratios of foliage phytic acid/total P of up to 90% leads to fundamentally different conclusions. We opted for exclusion for the following reasons. Four different methods are used to quantify phytic acid extracted from dry material using weak acids. The most common method (Appendix S1) is based on the action of phytic acid as a strong chelator, which binds positively charged ions like iron: Fe^{3+} is precipitated by phytic acid and the remaining Fe^{3+} can be quantified using colorimetry (Haug & Lantzsch 1983). According to our experience, phytic acid content, especially in leaf material, is overestimated with this method, probably because other negatively charged extract components may also bind Fe^{3+}. In addition, this method does not unambiguously distinguish phytic acid (InsP6) from other inositol phosphates, such as InsP4 and InsP5 (Lott *et al.* 2000). This problem is only partly overcome with method 2, which uses extract purification with ion exchange chromatography. The analysis with HPLC ion exchange chromatography (method 3) avoids these difficulties (Lehrfeld 1989), and yields correct estimates of phytic acid-P. A similarly reliable determination of P bound to phytic acid is achieved after enzymatic release of phosphate from phytic acid with phytases, followed by colorimetric determination of the released phosphate (method 4). In the last case, the results have to be corrected for inorganic phosphate in the extracts. The continued use of methods 1 and 2 is probably due to the fact that HPLC analysis and enzymatic phytic acid estimation are relatively time-consuming and costly. Considering that most results reported here were obtained with the ferric precipitation method, overestimates are very likely.

In the large majority of all studies considered in the present analysis, foliar phytic acid-P makes up < 10% of total P, maximum values reaching ca. 25%. We can conclude that phytic acid is ubiquitous in leaf tissue. Disregarding older studies with doubtful analytical capacities (McCance & Widdowson 1935), hardly any modern study that specifically tried to detect phytic acid in leaf tissue was unable to find this compound (*e.g.* Zhao *et al.* 2007). However, the amounts of phytic acid in leaves were indeed generally much lower than those of specialised storage organs (Lott *et al.* 2000; Raboy 2003). Unless the mentioned

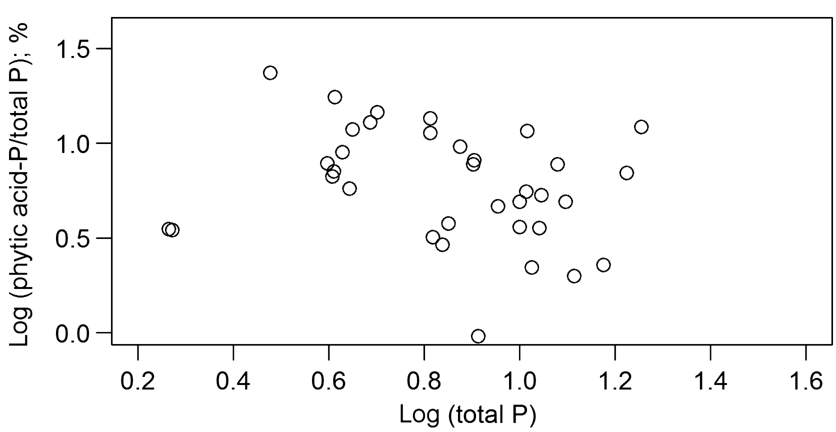

Fig. 2. Relationship of phytic acid-P (as percentage of total P) and total P in leaves. Data, which were log10-transformed, are averages of 35 species. The correlation is not significant ($P = 0.15$; Pearson Product moment correlation). The total data set with references is provided in Appendix S2.

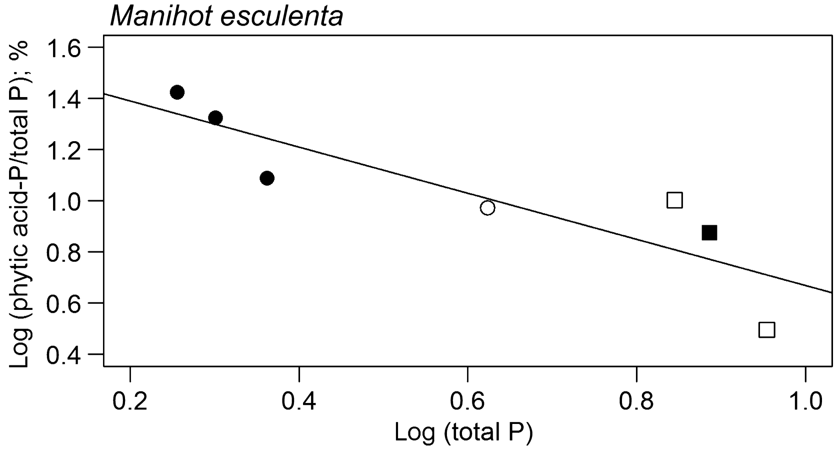

Fig. 3. Relationship of phytic acid-P (as percentage of total P) and total P in leaves of *Manihot esculenta*. Data, which were log10-transformed, are from four different studies. The regression line is significant (Pearson Product moment correlation, $P < 0.01$, $r^2 = 0.73$). Data are from four different sources (closed circles: Ravindran & Ravindran 1988; open circle: Ravindran *et al.* 1994; closed square: Udosen & Ukpanah 1993; open squares: Aletor & Adeogun 1995).

reports of very high ratios of phytic acid/total P in leaves (Abulude 2007; Kayode & Esiet 2007) receive independent validation in the future from unambiguous methods, the traditional view of low relative foliar phytic acid concentrations is supported in this review. However, until now very few wild plants have been studied in regard to their phytic acid content, in particular plants from nutrient-deficient habitats that have long-lived leaves. Hence, corroboration of the recent finding of high relative phytic acid concentrations in some epiphytic bromeliads (>20% of total P; Winkler & Zotz 2009) for a larger set of species could partly challenge our current understanding of the importance of phytic acid as a storage compound in leaves. Moreover, other important physiological and ecological functions of phytic acid in leaves at relatively low concentrations are also largely unexplored. For example, studies have shown that phytic acid can act as a herbivore deterrent (Green *et al.* 2001), but it is unclear how important this is for foliar protection in nature.

While the documented concentrations and proportion of phytic acid in leaves matched more or less our expectations, the lack of a positive correlation between the proportion of phytic acid and total P is enigmatic. Frequently, the amounts of phytic acid and total P are positively correlated in mature seeds and fruits (Eeckhout & Depaepe 1994) and also in leaves (Zhao *et al.* 2007). Similarly, the dynamic changes in P and phytic acid during the development of seeds (*e.g.* Greenwood *et al.* 1984; Batten & Wardlaw 1987) or other organs with storage functions (Samotus & Schwimmer 1962) also show an increasing proportion of phytic acid-P as total P increases. Although the regulation of phytic acid synthesis in plant tissue is not fully understood, the underlying mechanism may be rather simple: phytic acid synthesis is initiated when the uptake of P exceeds baseline needs for basic plant metabolism and no other sinks (growing shoots and roots, developing fruit or developing storage organs) are present (Bieleski 1973). Indeed, Mitsuhashi *et al.* (2005) showed that the synthesis of phytic acid in *Catharanthus roseus* cells was induced by growth in solutions with a high orthophosphate concentration, whereas little or no phytic acid was produced in cells growing under low external P conditions.

In view of the range of methods used in the compiled studies, with many potential errors when *e.g.* most of the commonly used procedures cannot unambiguously distinguish phytic acid (InsP6) from other inositol phosphates (Lott *et al.* 2000), or the relatively large scatter among the data, one could consider the lack of a correlation to be fortuitous, but a negative intra-specific trend found for *Manihot esculenta* is even more puzzling. Interestingly, a study with tobacco documented the levels of both acid-soluble organic P and total P for a range of fertiliser regimes (Kakie 1969), and detected a significant decrease in the ratio of the two in leaves with increasing P supply. Assuming that a large and relatively stable proportion of this organic P fraction represents phytic acid, this result would be consistent with the pattern detected for *M. esculenta*.

Moreover, the generally positive correlation between phytic acid and total P (Eeckhout & Depaepe 1994) is not universal in storage organs (Zhao *et al.* 2007). There are even examples for similar negative correlations: Oboh *et al.* (1989) analysed 49 varieties of sweet potato, in which phytic acid-P represented between 1% and 10% of total P. Analysing their data reveals a negative, highly significant correlation (Pearson Product Moment correlation on log-transformed data, $r^2 = 0.77$, $P < 0.001$). Data compiled in Lott *et al.* (2000) for nine species of cereal, like wheat, barley or rice, in which phytic acid-P accounts, on average, for 61–81% of total P, also show a negative correlation (Pearson Product Moment correlation, $r^2 = 0.68$, $P < 0.001$), while there is no such correlation for other dry seeds and fruits ($r^2 = 0.04$, $P > 0.05$, n = 23).

A really convincing explanation for these negative correlations is lacking. One study points to a possible role of leaf ontogeny: Ravindran & Ravindran (1988) found a decrease in total P and a proportional increase in phytic acid with leaf age in *M. esculenta*. However, with the exception of this and the study of Oboh *et al.* (1989), the analysed data always stemmed from different studies with varying methodologies, and a purely fortuitous reason cannot be excluded. To date, no study has explicitly looked at the effect of differences in P supply on leaf phytic acid levels. We are currently performing critical experiments with full factorial designs of different nutrient supplies of N and P using several species to address this question.

To conclude, we have compiled all available quantitative information on phytic acid in green leaves, confirming the general notion that it represents only a relatively low proportion of total P. However, there are some reports of very high phytic acid concentrations in leaves, which, if confirmed, would make it necessary to change our view of the role of phytic acid in leaves. Attention should also be directed towards the enigmatic finding of a negative correlation between phytic acid and total P, which has been documented too often for leaves and other plant organs as to make chance alone a satisfactory explanation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phytate-P concentrations in plant leaves

Appendix S2. Species averages of total P (in $mg \cdot g^{-1}$) and phytic acid-P (as % of total P) in leaves of different plant species

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