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REVIEW

Plant responsiveness to mycorrhizas differs from dependence upon mycorrhizas

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Abstract Soil phosphorus response curves of plants with and without mycorrhizas reflect two different, but complementary, phenomena. The first, plant responsiveness to mycorrhizas, is represented by the difference in growth between plants with and without mycorrhizas at any designated level of phosphorus availability. This is also a measure of mycorrhizal fungus effectiveness. The second, the lowest level of phosphorus availability at which plants can grow without mycorrhizas, is here termed dependence upon mycorrhizas. The latter definition differs from conventional usage which fails to distinguish dependence from responsiveness. Sigmoid curves generated by the three-parameter, logistic equation generally can model the responses of plants to mycorrhizas and phosphorus addition and can be used to assess responsiveness, effectiveness, and dependence. Such curves reveal that plant responsiveness or fungus effectiveness determined at a single level of phosphorus availability may be misleading when used to compare different host species' intrinsic capacities to respond to different mycorrhizal fungus species. Instead, the same relative position should be evaluated among phosphorus response curves for different species combinations. Dependence of a plant species known to benefit from mycorrhizas can be assessed with reference to only the phosphorus response curve of plants without mycorrhizas. Dependence is a constitutive property of plant species that can be used to classify them as facultatively or obligately mycotrophic. Dependence is a plant attribute upon which natural selection can act, but responsiveness and effectiveness cannot be selected directly because they are emergent properties of the interaction between plant and fungus species.

Keywords Logistic equation · Mycorrhizal fungus effectiveness · Mycotrophy · Phosphorus responsiveness · Plant growth depression

Introduction

Maturation of a scientific discipline is marked by the refinement of definitions of common concepts (Ford 2000). Definitions should enable terms to be used accurately and precisely: Everyone knows exactly what is meant, and there is little variation in how a term is applied. Imprecision arises when words in common usage with broad interpretations are used to denote technical concepts. "Responsiveness" of plants to mycorrhizal colonization, "dependency" of plants upon mycorrhizas, and "effectiveness" of mycorrhizal fungus species are terms commonly used in mycorrhiza research with a variety of meanings (e.g., Table 1).

I contend that the historic usage blends two different phenomena involved in the effects of mycorrhizal fungi and soil fertility on plant growth, and that each of these phenomena merits its own term. I suggest retaining "responsiveness" and "dependence" to denote them, but I advocate the use of "responsiveness" to designate what, in the past, predominantly has been termed "dependency" (Table 1). In contrast to much historic usage, I define "mycorrhiza dependence" as the inability of plants without mycorrhizas to grow or survive without some increase of

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Table 1 Historic usage of the terms “mycorrhiza dependency” and “mycorrhiza responsiveness”

Citation	Designation	Citation’s explanation or equation	Comments
Gerdemann 1975	Mycorrhiza dependency	No equation given. “Mycorrhiza dependency can be defined as the degree to which a plant is dependent on the mycorrhizal condition to produce its maximum growth or yield, at a given level of soil fertility. In order to determine mycorrhiza dependency of a particular species, one would need to compare the growth of mycorrhizal and non-mycorrhizal plants at various fertility levels and determine the level at which mycorrhizal and non-mycorrhizal plants grow equally well”	Gerdemann offers two important ideas: (1) that growth differences between *M* and NC plants need to be compared across a range of fertilities, and (2) that the fertility level at which growth or yield of *M* and NC plants is equal (*T*′ of Janos 1988) could be used as an index of mycorrhiza dependency
Barrow et al. 1977	Effectiveness of treatment (e.g., mycorrhizal inoculation) (C_M/C_{NC})	$Y = a - b \times \exp\left(-C_M[\mathrm{P}_M] - C_{\mathrm{NC}}[\mathrm{P}_{\mathrm{NC}}]\right)$ where Y=M or NC at each [P], [P] is the concentration of applied phosphorus, a is the maximum Y, and a–b is the performance at [P]=0	These authors fitted the Mitscherlich yield response equation to top dry weights of onions grown at 15 levels of applied phosphorus with or without mycorrhizas. The form of the equation they used assumes that the yields of mycorrhizal plants and plants without mycorrhizas are the same both when no phosphorus is applied and when phosphorus is not limiting. The ratio of the curvature coefficients (C_M/C_{NC}) with and without mycorrhizas represents the effectiveness of mycorrhizas in reducing need for applied phosphorus to achieve equivalent yields. Gazey et al. (2004) called this “mycorrhiza benefit”
Menge et al. 1978	Mycorrhizal dependency (relative mycorrhizal dependency)	=100×*M*/NC	This equation is to be applied “at a given level of soil fertility”. These authors define species that are never mycorrhizal as having no dependency. Range from 0% to +∞
Janos 1980a	Dependence on mycorrhizae for growth	No equation given. “The criteria used were ability of uninoculated plants to continue growth, and growth increase due to inoculation”	My purpose was to distinguish among facultatively and obligately mycotrophic plant species
Linderman and Hendrix 1982	VAM-responsive and VAM-dependent	No equation given. “A VAM-responsive host will exhibit enhanced growth at low P levels, but progressively reduced or no growth enhancement at high levels. A VAM-dependent host would exhibit enhanced growth by VAM up to abnormally high P levels indicating that, for practical purposes, it requires VAM to acquire adequate P”	This is the first usage I could find of “responsive” and “dependent”
Plenchette et al. 1983	Relative field mycorrhizal dependency (RFMD)	RFMD=100×(*M*−NC)/*M*	RFMD ranges from −∞ to 100%. These authors suggest that RFMD be superscripted with the quantity of available P in the soil
Janos 1984	Dependence	No equation given. “Species that are mycotrophic... may be facultatively or obligately dependent on mycorrhizae. These categories are the opposite ends of a	I presented a bar graph cartoon that represented plant species dependence as reflected by differences in the ability of plants without mycorrhizas

Table 1 (continued)

Citation	Designation	Citation's explanation or equation	Comments
		continuum along which species can be positioned according to their ability to grow with and without mycorrhizae at different levels of fertility"	to grow across a range of phosphorus fertilization levels (i.e., the bar graph was a discrete representation of Fig. 3c here)
Janos 1988	Dependence and responsiveness	No equation given but a schematic figure provided. "Either the threshold level of phosphorus below which plants without mycorrhizae do not appreciably grow (*T*), or the level above which there is no response to mycorrhizae (*T*′) measures plant 'dependence' on mycorrhizae for growth". "The difference between the curves (*R*) at any level of phosphorus, or integrated over all differences, measures plant 'responsiveness' to mycorrhizae"	This is the first formalization of the concepts used here, but now I have abandoned *T*′ as an index of dependence
Habte and Manjunath 1991	Mycorrhizal dependency (MD)	$\mathrm{MD}=100\times(M-\mathrm{NC})/M$ at 0.02 mg/l soil solution P concentration, in addition to responding to mycorrhizas significantly or not at 0.2 mg P/l	These authors' approach differs from that advocated here by basing five categories of dependency upon the growth difference between *M* and NC plants [i.e., index of Plenchette et al. (1983)] at just two levels of soil solution phosphorus concentration
Baon et al. 1993	Mycorrhizal response [also "mycorrhizal responsiveness = MR" as used by Zhu et al. (2001) with shoot phosphorus concentration as the measure of plant performance]	$=100\times(M-\mathrm{NC})/\mathrm{NC}$	This is the first equation designated "response" that I found. It sometimes is erroneously attributed (e.g., Bagyaraj 1992; Estrada-Luna et al. 2000) to Plenchette et al. (1983). This equation gives a value for response which always is 100% lower than the index of Menge et al. (1978), and which ranges from−100% to +∞
van der Heijden et al. 1998	Mycorrhizal dependency	$=1-((\text{mean NC}\times n)/\sum M$ of n treatments)	This is the index of Plenchette et al. (1983) expressed as a fraction. A single non-colonized treatment is compared to the performance of *n* mycorrhiza treatments with different inoculant fungus species. Its range is −∞ to 1
Gange and Ayres 1999	Plant benefit	$=100\times(m-\mathrm{NC})/\mathrm{NC}$	This approach allows calculation of the growth or yield advantage of mycorrhizas to individual plants when mycorrhizal and non-colonized individuals have not been paired. Its range is −100% to +∞
Siqueira and Saggin-Júnior 2001	Mycorrhizal dependency, mycorrhiza dependence, and plant responsiveness	Mycorrhiza dependency is the upper intersection point of best-fit linear or curvilinear regression lines for *M* and NC at Habte and Manjunath's (1991) soil solution P concentrations; the index of Plenchette et al. (1983) was used for responsiveness	These authors' dependence measure was used as a proxy for Janos' (1988) *T*′. Mycorrhizal dependency is expressed in units of soil solution P concentration
van der Heijden 2002	Mycorrhizal dependency	If $\sum M$ of n treatments$>\mathrm{NC}\times n$, then mycorrhizal dependency$=100\times(1-((\text{mean NC}\times n)/\sum M$ of n treatments)), but if $\sum M$ of n treatments$<\mathrm{NC}\times n$, then mycorrhizal dependency$=100\times(-1+(\sum M$ of n treatments$/(\text{mean NC}\times n)))$	An extension of van der Heijden et al. (1998) so that both beneficial and detrimental effects of mycorrhizas are scaled similarly. Its range is −100% to +100%

Table 1 (continued)

Citation	Designation	Citation's explanation or equation	Comments
Smith et al. 2003	Mycorrhizal growth dependency = MGD (also mycorrhizal P dependency = MPD)	$\mathrm{MGD}=100\times(m-\mathrm{NC})/m$	These authors apply the approach of Gange and Ayres (1999) in calculating MGD values (thereby enabling estimation of variance) for individual mycorrhizal plants, but they use the equation of Plenchette et al. (1983) which ranges from $-\infty$ to 100%
This paper	Responsiveness = $R_{[\mathrm{P}]}$, and dependence = D	$R_{[\mathrm{P}]}=M-\mathrm{NC}$ for designated concentrations of available phosphorus ([P]) indicated as a subscript $D=(-1/S)\times\ln(0.9AI/(0.1A^2-0.1AI))$ with S, I, and A as defined for Eq. (1) (see text)	The indicated equation is for absolute responsiveness, which can be relativized as done by either Plenchette et al. (1983) or Baon et al. (1993). Dependence is calculated from a logistic equation fitted to the phosphorus response curve of plants without mycorrhizas

In all cases except Janos (1988), Siqueira and Saggin-Júnior (2001), perhaps Gerdemann (1975), and perhaps Linderman and Hendrix (1982), regardless of their designation of "dependency" (e.g., Plenchette et al. 1983) or "response" (e.g., Baon et al. 1993), the cited authors are indexing what I suggest calling "responsiveness". "Designation" shows the terminology used by the cited reference. Where an equation for a designated term was given, for consistency, I have replaced original symbols with "*M*" for the mean performance (e.g., growth, dry biomass, phosphorus concentration, seed yield) of mycorrhizal plants and "NC" for the mean performance of plants that are not colonized by mycorrhizas. As subscripts, those abbreviations similarly denote plants with and without mycorrhizas, respectively. I use "NC" (non-colonized) in preference to "NM" which commonly is used to denote "non-mycorrhizal" because the latter can be ambiguous, as it may refer to either a normally mycorrhizal species lacking mycorrhizas or a non-mycotrophic species which never forms or benefits from mycorrhizas (see Tester et al. 1988). *C* the curvature coefficient of a Mitscherlich yield response equation; *n* number of treatments (e.g., inoculation with different fungus species separately); *m* the plant performance parameter of an individual mycorrhizal plant. The ranges of possible values listed for indices for which equations are given reflect that mycorrhizas can affect host performance negatively

soil fertility. As discussed herein, this distinction applies responsiveness and dependence to separable attributes of the mycorrhiza symbiosis. Mycorrhiza dependence can be assessed by examining the effects of a range of soil fertilities (especially, that of available phosphorus) on the performance of plants lacking mycorrhizas. Stated another way, the necessity of mycorrhizas (i.e., dependence) can be inferred from the inability of plants lacking mycorrhizas to respond to applied phosphorus.

I recognized that complementary phenomena are involved in the effects of mycorrhizas and soil fertility on plant performance when I compared the growth with and without arbuscular mycorrhizas (AM, used generically to include both vesicular–arbuscular and strictly arbuscular forms) of 28 species of tropical plants (Janos 1980a). Many of the plant species I tested, including most large-seeded, mature forest tree species, became moribund without mycorrhizas (Fig. 1a,b) at a size that was correlated with seed weight, and presumably with seed mineral nutrient reserves (Janos 1980a). Some of these species, however, grew so slowly even with mycorrhizas that growth stimulation by mycorrhizas could not be discerned for several months (Janos 1975, 1977, 1980a). In contrast, pioneer forbs, shrubs, and small, light-wooded trees often were able to grow without mycorrhizas at the prevailing low level of soil fertility, but mycorrhizas accelerated their growth (Fig. 1c,d), presumably by enhancing uptake of the limiting mineral nutrient, phosphorus. Thus, the magnitude of plant growth improvement by mycorrhizas (i.e., responsiveness, as used here) is somewhat independent of the ability of plants to grow without mycorrhizas (i.e., dependence). This led me to differentiate concepts of "responsiveness" and "dependence" by means of discrete (Janos 1984) and continuous (Janos 1988) graphical models.

Subsequent to my explicit suggestion that dependence and responsiveness are different (Janos 1988), Sieverding (1991) clarified my continuous model by presenting it as four separate graphs (his Fig. 2.5). He illustrated that of the four possible combinations of low versus high dependence and low versus high responsiveness, high responsiveness cannot occur with low dependence. In Fig. 2, I have modified his illustration by using a logistic model of plant response to phosphorus, and I show indices for plant dependence upon mycorrhizas (*D*) and responsiveness to mycorrhizas ($R_{\max}$, not relativized; and the relativized indices of Menge et al. (1978) and Plenchette et al. (1983) calculated for $R_{\max}$). Boerner (1992) accepted and

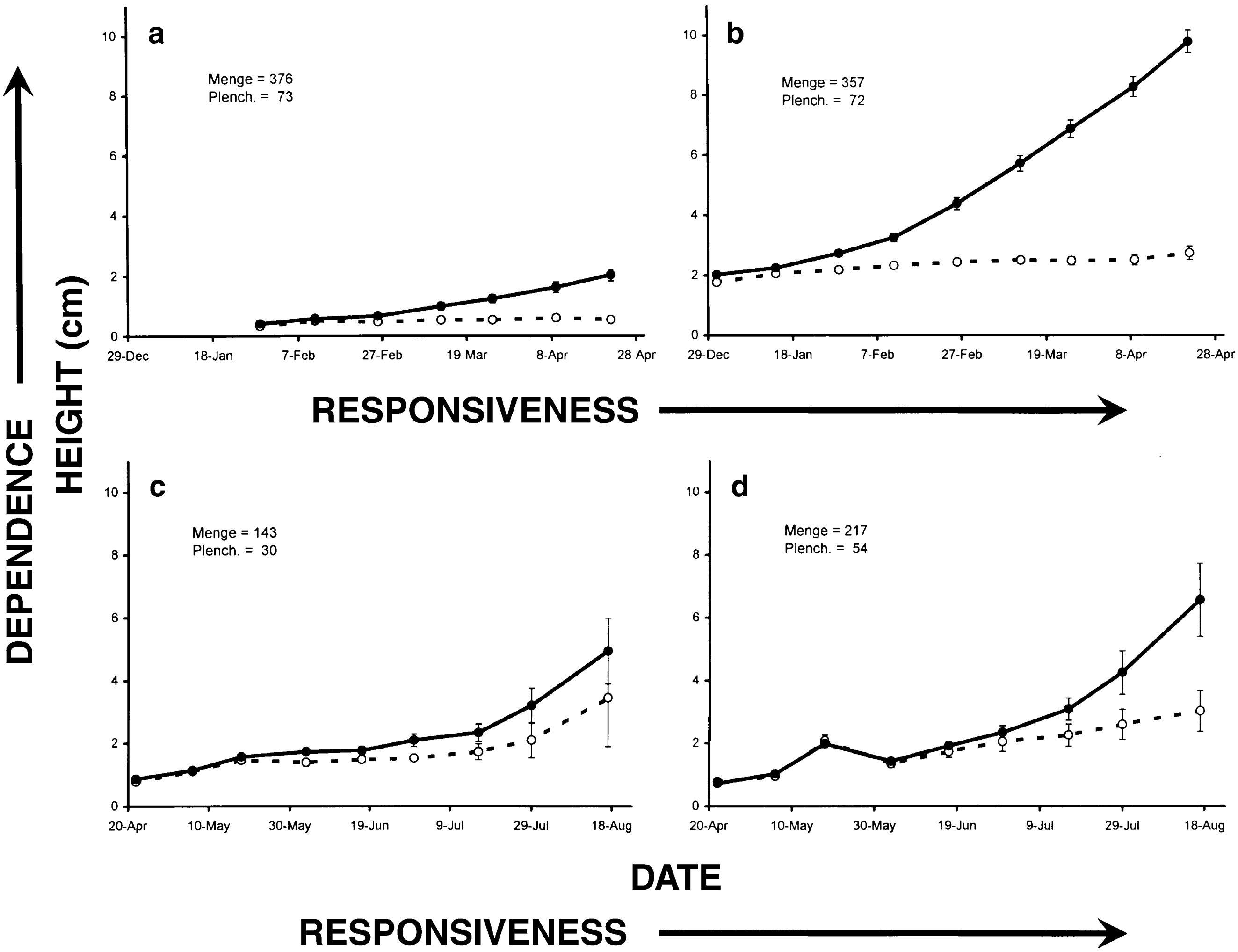

Fig. 1 Mean height increase (±1 SE) of four tropical plant species inoculated with arbuscular mycorrhizal fungi (*solid points and lines*) or not inoculated (*open points and dashed lines*) at a single, low level (about 6 mg/kg Olson phosphorus) of phosphorus availability (data from Janos 1980a). Two indices of relative "mycorrhizal dependency" (%; see Table 1; these are indices of responsiveness as used here), those of Menge et al. (1978) ("Menge") and Plenchette et al. (1983) ("Plench."), calculated based upon final heights, are shown for each species. The inability to grow when without mycorrhizas of species **a** and **b** suggests that they are more dependent upon mycorrhizas for growth than are species **c** and **d**. Species **b** and **d** have higher absolute responsiveness to mycorrhizas than species **a** and **c**, respectively (the responsiveness axis scale for **a** and **b** differs from that for **c** and **d**). **a** *Carludovica palmata* R. & P. (Cyclanthaceae); **b** *Psidium guajava* L. (Myrtaceae); **c** *Ficus glabrata* H.B.K. (Moraceae); **d** *Solanum rugosum* Dunal. (Solanaceae)

correctly applied the distinction between these concepts, and Siquiera and Saggin-Júnior (2001) attempted to test their utility.

In this study, I refine my (Janos 1988) continuous model by fitting the logistic equation to mycorrhizal and non-colonized plant responses to phosphorus, and I use the model to clarify the relationships among responsiveness, dependence, fungus effectiveness, facultative mycotrophy, and obligate mycotrophy. My terminology departs from historical usage of "dependency" by Gerdemann (1975), Menge et al. (1978), and Plenchette et al. (1983) among others, but I argue that it is semantically accurate. Although I hope for acceptance of this terminology, my minimum objective is to have authors explicitly state what they mean by whichever term they choose.

Modeling plant species responses to phosphorus

Phosphorus is the limiting mineral nutrient in many natural and some crop systems, and both arbuscular mycorrhizas and ectomycorrhizas are well known to enhance host phosphorus nutrition (Smith and Read 1997). I will develop my model with respect to AM and a gradient of phosphorus availability, but it also may fit other mycorrhiza types and perhaps other mineral nutrients. However, the model is only

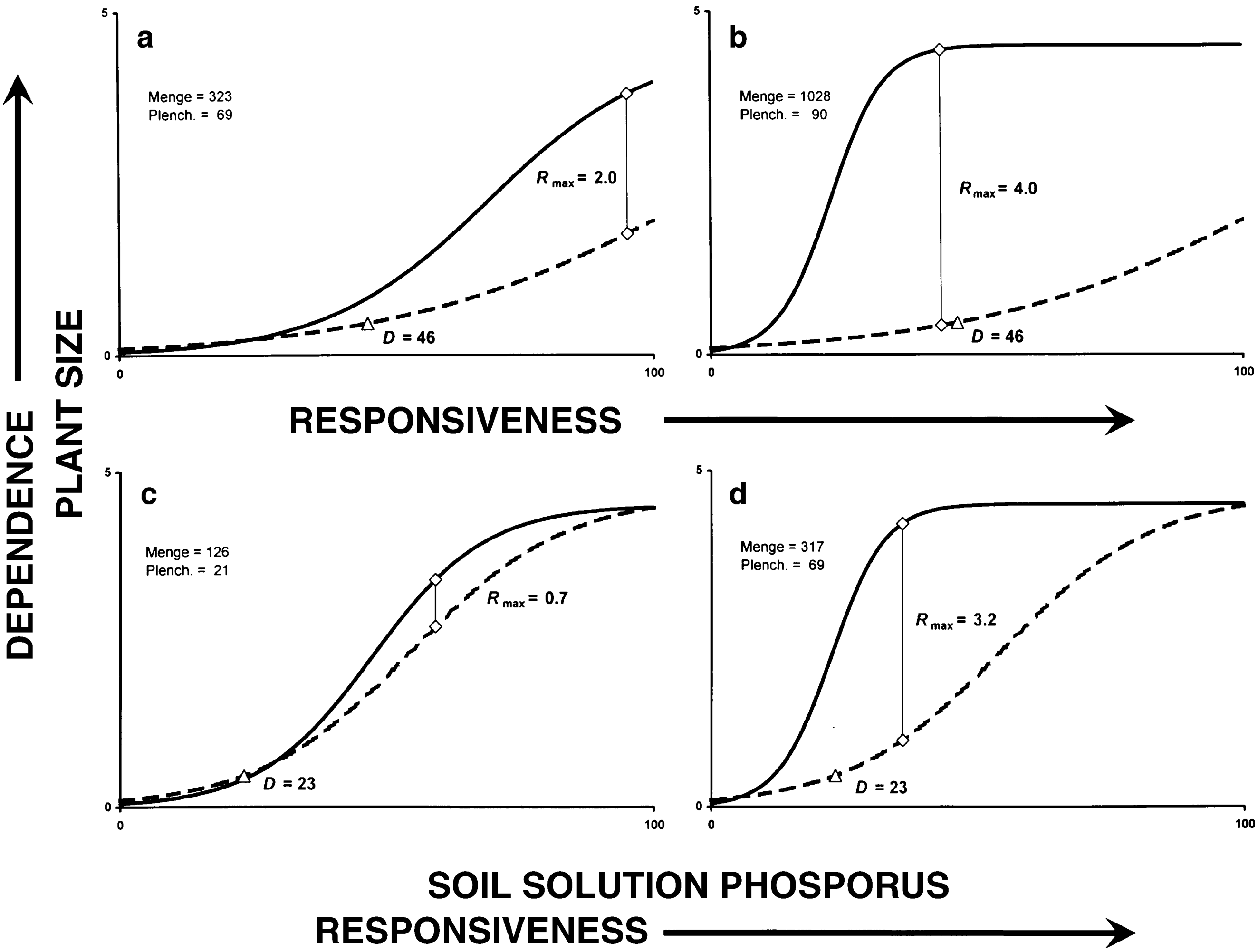

Fig. 2 Phosphorus response curves for four hypothetical facultatively mycotrophic plant species with (*solid lines*) and without (*dashed lines*) mycorrhizas (after Sieverding 1991). Dependence upon mycorrhizas (*D*, *open triangles*), expressed in units of available phosphorus, is the level of phosphorus required to produce non-colonized plants that are 10% larger than their asymptotic, minimum size. The species depicted as **a** and **b** are equally dependent upon mycorrhizas and exceed the dependence of **c** and **d** which equal one another in dependence. Absolute maximum plant responsiveness to mycorrhizas (R_{max}, *solid vertical line connecting open diamonds*), which is one of many absolute responsiveness values that can be calculated over a tested range of phosphorus availabilities, is expressed in units of plant size. The relative "mycorrhizal dependency" indices (%) of Menge et al. (1978) ("Menge") and Plenchette et al. (1983) ("Plench."), are shown for maximum responsiveness (R_{max}) of each species. The species depicted as **b** and **d** are more responsive to mycorrhizas than are **a** and **c**, respectively (the responsiveness axis scale for **a** and **b** differs from that for **c** and **d**)

applicable to a plant growth-limiting nutrient element for which mycorrhizas improve acquisition. Mineral nutrients other than that modeled must not be limiting.

Barrow et al. (1977) fitted curvilinear functions to the dry weights of mycorrhizal and non-colonized plants grown at several phosphorus availabilities. Their purpose was to broadly compare plant yields across multiple rates of phosphorus application in contrast to the usual "big plant, little plant" experiment (Smith and Read 1997) typically conducted at a single level of phosphorus availability. A single phosphorus level experiment provides just one vertical comparison to measure growth enhancement by mycorrhizas. Subsequent papers that used the approach of Barrow et al. (1977) (e.g., Pairunan et al. 1980; Abbott and Robson 1984) focused upon a second comparison, that between mycorrhizal plants and similarly sized plants lacking mycorrhizas which were provided with supplemental phosphorus. Such a comparison along the horizontal axis answers the question, "How much phosphorus fertilizer are mycorrhizas worth?" Because there are practical constraints on the number of levels of phosphorus availability that can be incorporated in an experiment, and because plant responses to phosphorus are usually curvilinear on non-transformed axes, these authors (Pairunan et al. 1980; Abbott and Robson 1984) needed precise equations for interpolation among tested phosphorus levels.

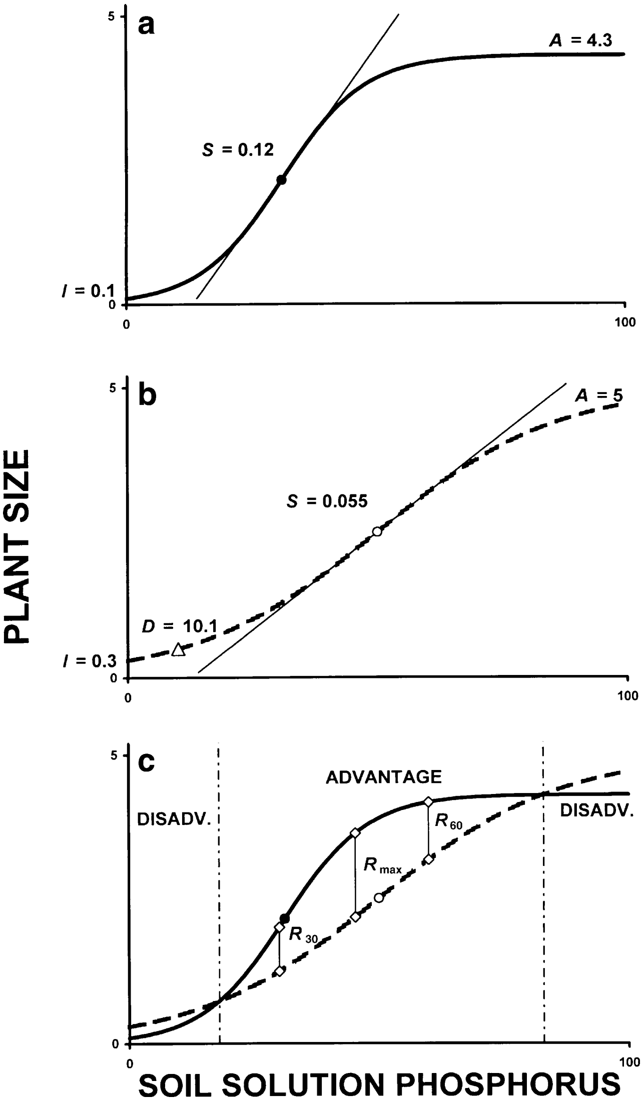

Fig. 3 Hypothetical generalized phosphorus response curves corresponding to Eq. (1) for a single facultatively mycotrophic plant species with (*solid lines*) and without (*dashed lines*) mycorrhizas showing inflection points (P_{ip}) as a *filled circle* and an *open circle*, respectively. **a** depicts the response of plants with mycorrhizas, and shows the curve parameters: the minimum growth intercept (I), the slope (S, the tangent at the inflection point), and the asymptote (A). **b** depicts the response of plants without mycorrhizas, shows curve parameters, and illustrates an index of dependence (D), which represents 10% of the asymptotic size (A) of plants without mycorrhizas. **c** The curves of **a** and **b** are combined to illustrate regions (separated by *vertical broken lines*) in which mycorrhizas are beneficial for plant growth (ADVANTAGE) or disadvantageous (DISADV.). In **c**, plant absolute responsiveness to mycorrhizas is shown as *solid vertical lines* connecting *open diamonds* for three levels (30, 45.3, and 60 units) of soil solution phosphorus (R_{30}, R_{max}, and R_{60}, respectively). Absolute maximum responsiveness to mycorrhizas (R_{max}; expressed in units of the measured plant size parameter) reflects the greatest positive difference between the two curves

Besides making a horizontal comparison, there is another reason to fit curves to plant responses. If the same equation can be fitted to the responses of plants with and without mycorrhizas, then the complex interaction of mycorrhizas and phosphorus can be investigated by examining how their fitted equation parameters differ (e.g., Pairunan et al. 1980). Bolan et al. (1983), however, found that different equations gave the best fit depending upon the presence or absence of mycorrhizas, plant root attributes, and soil phosphate adsorption capacity. Abbott and Robson (1984) followed Campbell and Keay (1970) in fitting exponential (=Mitscherlich) yield response equations to their data. Nevertheless, Campbell and Keay (1970) had noted that phosphorus response curves can be grouped into three general forms: (1) sigmoid; (2) a large response to low phosphorus with rapid attainment of a plateau (e.g., exponential or hyperbolic); and (3) yield depression at high phosphorus.

Campbell and Keay (1970) considered only forbs (clover, lupin, ryegrass) that may be expected to respond to phosphorus regardless of mycorrhizal status. In contrast, some obligately mycotrophic tropical tree species are unable to grow without mycorrhizas across a range of phosphorus availabilities (Siqueira and Saggin-Júnior 2001), and neither exponential nor hyperbolic functions can fit such non-responsiveness to applied phosphorus. Siqueira and Saggin-Júnior's (2001) solution was to fit different equations to the responses of mycorrhizal and non-colonized plants. Although their approach allowed calculation of the upper intersection point of the phosphorus response curves for these two groups of plants, the parameters of their different equations could not be compared directly.

The most broadly applicable equations for plant responses to phosphorus and mycorrhizas are those for sigmoid curves (Fig. 2; see also Fig. 4). Although they may not fit data as closely as other equations in all instances, they can accommodate both very rapid initial rises and long initial lags, and so can model responses to phosphorus of both mycorrhizal and non-colonized obligate mycotrophs. They cannot reflect yield depression at high phosphorus because they ascend to an asymptote, but such high phosphorus levels are beyond the upper bound of my model. When high phosphorus depresses yield, phosphorus no longer is the limiting nutrient, and it even may interfere with the availability of other nutrients (see Howeler et al. 1982).

Others have used equations that generate sigmoid curves to model aspects of mycorrhizal associations. McGonigle (2001) used one form of the well-known logistic (=Verhulst) equation to model changes in AM colonized root length over time. Declerck et al. (2001) compared two-, three-, and four-parameter sigmoid equations, including the logistic, applied to data on AM fungus spore production in root organ culture. The four-parameter Schnute equation most closely fitted their experimental data (Declerck et al. 2001), but its parameters do not have intuitive biological analogs if used to model plant responses to phosphorus.

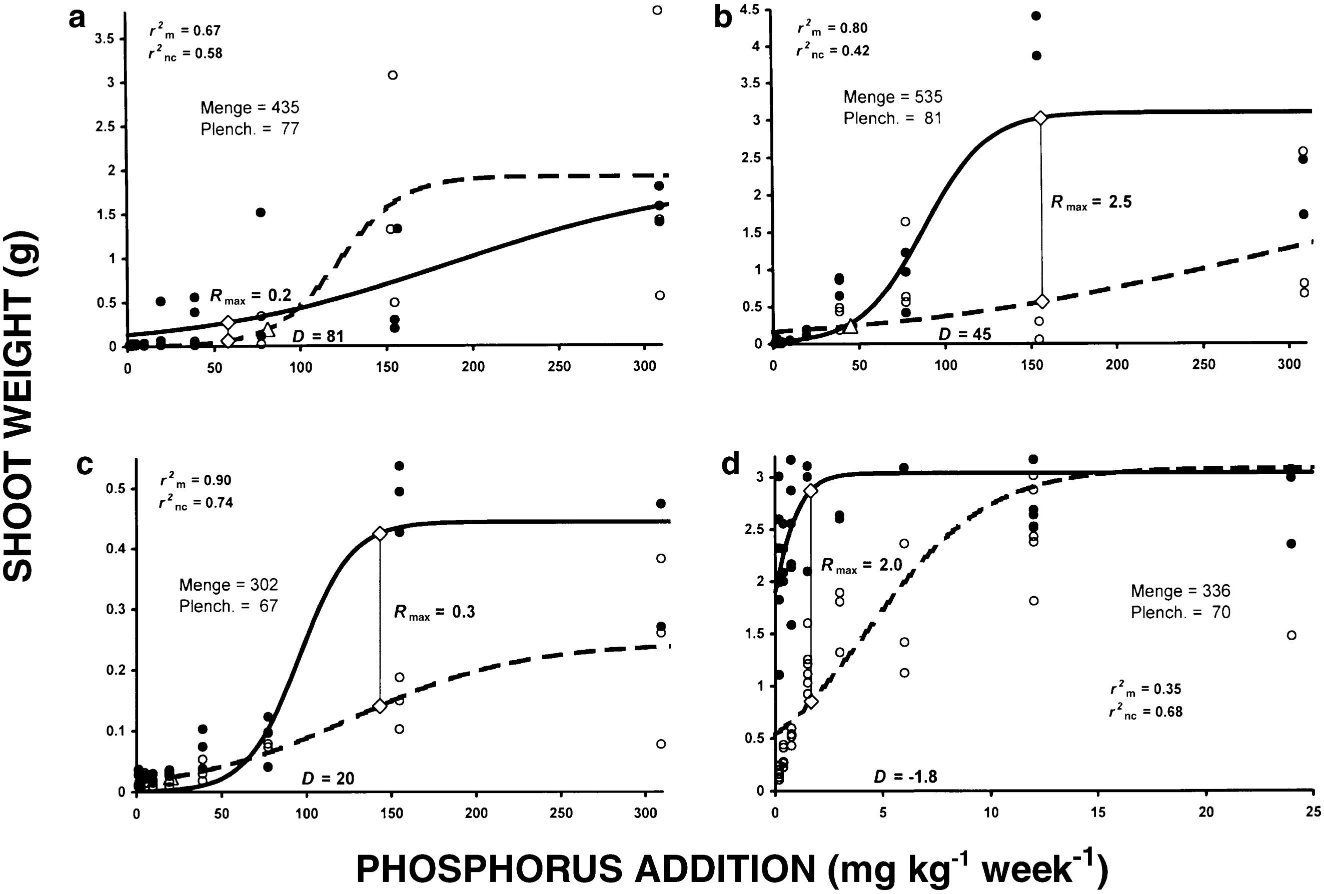

Fig. 4 Phosphorus response curves corresponding to Eq. (1) fitted to shoot dry weights of four plant species inoculated with mixed AM fungi (*filled circles* and *solid lines*) or not inoculated (*open circles* and *dashed lines*). Coefficients of determination (r^2) are subscripted *m* for mycorrhizal and *nc* for non-colonized. An index of dependence upon mycorrhizas (*D*), which represents 10% of the asymptotic size of plants without mycorrhizas, is shown, as is absolute maximum plant responsiveness to mycorrhizas ($R_{\max}$, *solid vertical line* connecting *open diamonds*). The relative "mycorrhizal dependency" indices (%) of Menge et al. (1978) ("Menge") and Plenchette et al. (1983) ("Plench.") are given for maximum responsiveness ($R_{\max}$) of each species. **a**, **b**, and **c** *Coriandrum sativum* L. (Apiaceae), *Lycopersicon esculentum* Mill. (Solanaceae), and *Capsicum annuum* L. (Solanaceae) all grown as one plant per 8-l pot with three pots per treatment after 10.5, 8, and 8 weeks, respectively in a tropical Andosol (about 3 mg/kg Olson phosphorus) at nine rates of weekly soluble phosphorus addition (see Schroeder and Janos 2004). **d** *Tanacetum cinerariifolium* (Trevir.) Schultz-Bip. (Asteraceae) grown as one plant per 400-ml pot (one to seven surviving plants per treatment at harvest) after 37 weeks in a temperate-zone forest soil and sand mix (about 50 mg/kg Olson phosphorus) at nine rates of weekly soluble phosphorus addition. In **d**, the fitted equations for each group were constrained to pass through the mean shoot dry weight at the highest (48 mg kg^{-1} week^{-1}; not shown) level of applied phosphorus. Species **a** through **c** decline in relative mycorrhiza dependence (D=81, 45, 20 mg kg^{-1} wk^{-1}, respectively). Species **d** cannot be compared directly to the others because it was grown under different conditions

Because of its interpretability for modeling plant responses to phosphorus, I suggest using the logistic equation, which commonly is employed to model the growth of populations through time:

$$W = A/(1 + b \times \exp(-SP)), \text{ where } b = (A - I)/I \qquad (1)$$

In this equation, the response variable *W* represents shoot dry weight, total plant dry weight, or another measure of plant size, and *P* is the amount of soil solution (or added) phosphorus. The equation is completely determined by its three parameters: (1) *I*, the *y*-axis intercept (which, in population growth models, corresponds to initial population size); (2) *A*, the asymptote (the carrying capacity for a population); and (3) *S*, the slope of a tangent at the inflection point (the intrinsic rate of increase of a population). When used to model plant response to phosphorus (Fig. 3), these parameters represent: (1) seedling size as determined by seed phosphorus reserves (and mycorrhiza carbon cost to mycorrhizal seedlings; *I*); (2) the maximum growth attainable during a fixed-length experiment with phosphorus not limiting (i.e., plant growth rate is maximized under the conditions of the experiment, thereby setting the upper asymptote of size; *A*); and (3) the maximum rate of change of growth rate in response to changing phosphorus availability (*S*).

McGonigle (2001) employed a form of the logistic equation that incorporated the position of the inflection point as a parameter instead of the *y*-axis intercept. Because

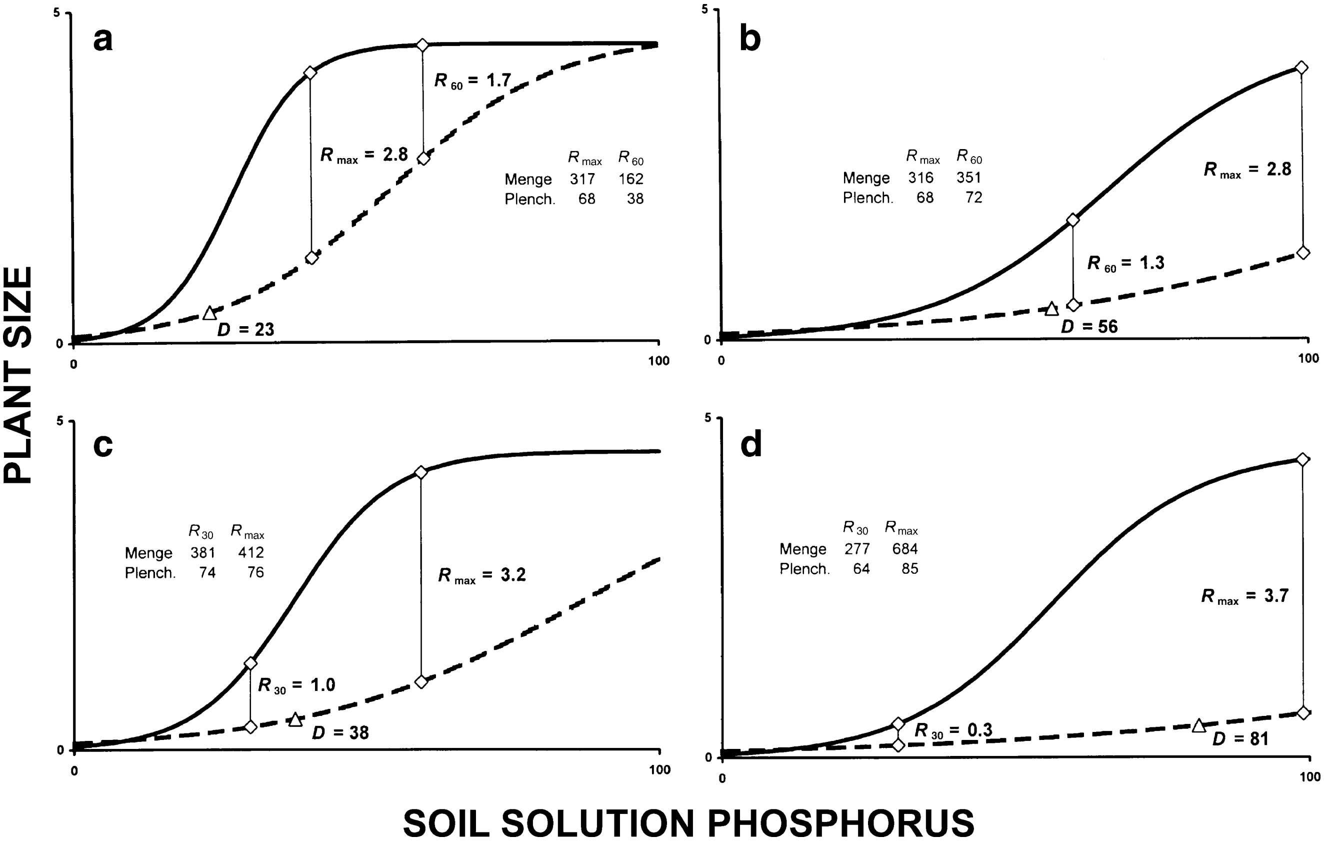

Fig. 5 Phosphorus response curves for four hypothetical facultatively mycotrophic plant species (symbols as in Fig. 3). The relative "mycorrhizal dependency" indices (%) of Menge et al. (1978) ("Menge") and Plenchette et al. (1983) ("Plench.") are shown for absolute maximum responsiveness (R_{max}) and absolute responsiveness at 30 (R_{30}) or 60 (R_{60}) units of phosphorus. **a** and **b** illustrate that two species with identical absolute maximum responsiveness can differ in responsiveness when assessed at another single phosphorus level (R_{60}). **c** and **d** illustrate that the species (**c**) with highest responsiveness assessed at a single phosphorus level that does not maximize responsiveness (R_{30}) may be least responsive at R_{max}

the curve is completely determined by three parameters, however, the phosphorus level at which the inflection point occurs (P_{ip}) can be calculated from I, A, and S as:

$$P_{ip} = (-1/S) \times ln(I/(A-I)) \tag{2}$$

The latter parameter (P_{ip}) may closely approximate the optimum level of phosphorus for its most efficient utilization in producing biomass (i.e., the most biomass increase per unit increase of phosphorus content; see Koide 1991), provided that tissue phosphorus content increases with increased substrate phosphorus availability. More than this amount of phosphorus has a progressively diminishing effect on growth rate (Fig. 3), suggesting that phosphorus is beginning to saturate and that "luxury" phosphorus might accumulate in plant tissue. The major, unverified assumption implicit in fitting Eq. (1) to plant phosphorus responses is that those responses are symmetric around the inflection point. If they are not, that will be reflected by unacceptably low coefficients of determination of fitted curves.

Several choices must be made in designing an experiment to determine phosphorus response curves. Artificial versus natural substrates and a single addition of solid phosphorus fertilizer versus repeated additions of phosphorus in solution must be selected. It is difficult to know how much phosphorus is leached, how much is immobilized, and how much actually is available for uptake by plants and mycorrhizas. Just as there are many different methods (extractants) to measure plant "available" phosphorus, the amount of phosphorus available to plants across an addition series at best may be an approximation. As long as phosphorus additions produce differing availabilities reflected by differential plant growth, they will serve adequately. Nevertheless, cross-experiment or cross-soil comparisons are likely to be problematic. Generalization will require comparisons of plant species under similar conditions and protocols using substrates that are sufficiently lacking in phosphorus to reveal full sigmoid curves.

In Fig. 4, I have fitted logistic curves to data for two herbaceous annuals, *Coriandrum sativum* L. (Fig. 4a) and *Lycopersicon esculentum* Mill. (Fig. 4b), and two small, bushy perennials, *Capsicum annuum* L. (Fig. 4c) and *Tanacetum cinerariifolium* (Trevir.) Schultz-Bip (Fig. 4d). All were grown with periodic additions of complete nutrients minus phosphorus and separate weekly additions of different amounts of phosphorus in solution [see Schroeder and Janos (2004) for details regarding Fig. 4a–c]. Because the easiest, most accurate way to produce multiple levels of phosphorus in solution is by serial dilution, all four species were provided geometric series of phosphorus additions. *C. sativum*, *L. esculentum*, and *C. annuum* were grown in a tropical soil with a high capacity to immobilize phosphorus, and were supplemented with as much as 309 mg of phosphorus per kilogram of soil each week until harvest at 2 to 2.5 months after transplant. The low phosphorus availability of the non-amended soil (about 3 mg/kg Olson P) allowed full phosphorus response curves to be obtained for plants without mycorrhizas. *Tanacetum cinerariifolium* was grown in a relatively fertile substrate (about 50 mg/kg Olson P) that did not immobilize phosphorus, and so, the phosphorus response curves of both plants with and without mycorrhizas are truncated. Logistic curves generally fit the data well, explaining 58% or more of the variation in shoot weight, except for mycorrhizal *T. cinerariifolium* $\left(r_m^2 = 0.35\right)$ and non-colonized *L. esculentum* $\left(r_{nc}^2 = 0.42\right)$. For *T. cinerariifolium*, there is greater scatter among mycorrhizal than among non-inoculated plant weights, which suggests that the poor fit to mycorrhizal plant data is predominantly influenced by variance among individuals within phosphorus levels instead of reflecting inadequacy of the logistic model. The non-inoculated *L. esculentum* fit is greatly diminished by two exceptionally small plants at the second highest level of phosphorus addition.

Generalized effects of phosphorus availability and mycorrhizas

Sigmoid models of the responses to phosphorus of plants with and without mycorrhizas may have an underlying biological basis. Very low levels of available phosphorus could be below plant thresholds for uptake (Howeler et al. 1982; Bolan et al. 1983; see Bolan 1991), thereby producing a low *y*-axis intercept (*I*). As available phosphorus is increased, the numerous physiological processes dependent upon it may compete with one another for the element, but this biochemical competition should diminish with increasing supply until the slope of a tangent to the curve (*S*) is maximized at the inflection point (P_{ip}). Although plant growth rate continues to increase until it is maximized at the asymptote (*A*), above the inflection point, the response of growth rate to increasing phosphorus diminishes as the intrinsic maximum rates of phosphorus-requiring physiological processes are reached. At the asymptote, something other than phosphorus limits growth.

Although the biological bases of a sigmoid response may apply similarly to plants with and without mycorrhizas, the shapes and positions of their curves usually will differ. The general model that I postulate has three regions defined by the two possible intersection points of the phosphorus response curves for plants of a single species with and without mycorrhizas (Fig. 3c). At the lowest levels of phosphorus availability and at the highest, mycorrhizas might depress plant growth and thereby be disadvantageous to the plant species. Between the intersection points of the two curves, mycorrhizas produce their well-known advantage for plant growth.

Numerous “big plant, little plant” publications report plant growth improvement attributable to mycorrhizas, and such “mycorrhiza advantage” is thought to have fostered the evolution of mycotrophism (literally, “fungus nourishment”—reliance by plants upon mycorrhizal fungi for mineral nutrition). Thus, the middle region of my general model is well supported.

At least two dozen published papers describe growth depression caused by mycorrhizas at high levels of phosphorus availability (see Abbott and Robson 1984; Cooper 1984; Jakobsen 1999). Thereby, mycorrhiza disadvantage at high phosphorus is supported, although it need not occur if plants reject mycorrhizas. In the latter instance, the asymptotes of inoculated and non-colonized plants will be the same (although the phosphorus response curve for inoculated plants should be truncated, stopping at the phosphorus level above which mycorrhizas do not form). When low light or low temperature do not limit photosynthesis (Smith and Smith 1996), mycorrhiza disadvantage at high phosphorus is most likely if colonization is little suppressed [which may have been the case for *C. sativum* (Fig. 4a; see Schroeder and Janos 2004)]. Minimal suppression of colonization may occur if phosphorus availability is elevated after many mycorrhizas already have formed, or if phosphorus availability fluctuates temporally (for example, because of periodic additions of soluble phosphorus to a phosphorus immobilizing soil). In either case, if supplies of other mineral nutrients are adequate, then host growth is likely to be carbon-limited (Fitter 1991), and the growth of mycorrhizal plants will be depressed because of carbon “loss” to fungus associates (Jakobsen 1999).

A few published observations support mycorrhiza disadvantage at low phosphorus availability. Crush (1973) reported that *Rhizophagus tenuis* [=*Glomus tenue* (Greenhall) Hall] diminished the growth of three grass species in a soil with 8 mg/kg Truog phosphorus, which he attributed to the fungus competing with its host for the limited available phosphorus. Jakobsen (1999; his Table 4) reported that the AM fungus *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders diminished growth and phosphorus concentration of wheat at low phosphorus availability (8–10 mg/kg Olsen phosphorus; Jakobsen, personal communication). Graham and Abbott (2000) found that eight AM fungus isolates diminished wheat growth at 4 mg/kg Olson phosphorus. Kahiluoto et al. (2000) found that a field soil AM fungus community diminished the growth of both flax and barley at 2.8 mg/kg water extractable phosphorus. Burleigh et al. (2002) reported that tomato growth was diminished by *Gigaspora rosea* Nicol. & Schenck and *Glomus caledonium* (Nicol. & Gerd.) Trappe & Gerd. at 19.6 mg/kg added phosphorus.

Growth depression by mycorrhizas at low phosphorus availability might result from competition between mycorrhizal fungi and their hosts for the little available phosphorus as Crush (1973) suggested, but it also could be a consequence of demand by the fungi for fixed carbon from the host. If so, growth depression is likely to be transient (e.g., Bethlenfalvay et al. 1982; Koide 1985). In early seedling growth when plants are relying upon seed stores of phosphorus but have little leaf area and may be carbon-limited, seedlings without mycorrhizas may be larger than those with them. The presence of leachable substances in the seed coats of some legumes (e.g., Trotman and Weaver 2000) that may inhibit nodulation during earliest seedling growth suggests that the carbon demand of a root symbiont (rhizobium) can be detrimental to very young seedlings. When seed stores of phosphorus are depleted and phosphorus supplants carbon as the element limiting seedling growth, however, mycorrhizas may enhance plant growth, especially if increased extra-matrical hypha length improves access to phosphorus. Whether or not common mycorrhizal networks (Leake et al. 2004) and potential consequent reduction of the cost of mycorrhizal fungus associates, or even carbon supply from the fungi to a host plant (Simard et al. 2002) preclude growth depression at low phosphorus in natural communities merits investigation.

Persistent growth depression at low phosphorus availability might occur if mycorrhizal fungus species are incompatible with hosts such as some crop cultivars (see Graham and Abbott 2000) or if seedlings are moribund even with mycorrhizas. That may be unlikely, except in artificial substrates or with plant species grown at unnaturally low levels of phosphorus availability. In native soils, natural selection for mycotrophy probably tends to eliminate the lower intersection point of phosphorus response curves (effectively by shifting it to the left).

In pot experiments, the full range of phosphorus response curves (from mycorrhiza disadvantage through advantage to disadvantage; Fig. 3) may not be seen unless an artificial substrate such as acid-washed sand is used to facilitate provision of very low phosphorus availabilities. In moderately fertile natural substrates, full curves may not be obtained because of truncation at low phosphorus addition (e.g., Fig. 4d). If the growth of plants without mycorrhizas is limited by something other than phosphorus, then mycorrhizal and non-colonized plant phosphorus response curves may not have an upper intersection point (possibly an explanation for Fig. 4c).

For a single plant species, if the P_{ip} of mycorrhizal plants is to the left of that for plants without mycorrhizas (i.e., at lower P) as is typical, then growth benefit from mycorrhizas will result. But whereas sufficient, that condition is not necessary for there to be a growth benefit (e.g., Fig. 4a). Typically, S is greater for mycorrhizal plants than for those without mycorrhizas (Fig. 4b–d; see Koide 1991), but this is neither necessary nor sufficient for mycorrhizas to confer a growth benefit. Just as the phosphorus response curves for a single plant species with and without mycorrhizas are likely to differ, if different plant species are grown in the same substrate with the same mycorrhizal fungi those plant species' phosphorus response curves also are likely to differ in position.

Definitions of responsiveness, effectiveness, and dependence

Responsiveness to mycorrhizas and dependence upon mycorrhizas can be defined with reference to the generalized phosphorus response curves of plants with and without mycorrhizas (Fig. 3). Two phenomena can be assessed separately with these response curves. The first phenomenon involves both curves and is the usual vertical comparison that I call "responsiveness". The second phenomenon, which I call "dependence", is assessed with reference only to the phosphorus response curve of plants lacking mycorrhizas. It involves their ability to grow in the absence of mycorrhizas (i.e., dependence upon mycorrhizas is inferred from plant inability to respond to small amounts of applied phosphorus). *Thus, the essential distinction between the two phenomena is that the first is a conjoint property of a plant species interacting with a mycorrhizal fungus or fungi, but the second is strictly a property of a plant species or genotype*. What term to use for each of these phenomena is a semantic question, but because the phenomena differ, different terms are needed.

Although Menge et al. (1978), Plenchette et al. (1983), and many others following them designate the vertically relativized size or size difference of plants with and without mycorrhizas at a given level of phosphorus availability as "relative mycorrhizal dependency" (see Table 1), they fail to distinguish the two phenomena of concern. A dictionary consultation indicates that "responsiveness" involves a reaction to something, whereas "dependence" involves an inability to exist or function without something. Therefore, I contend that the usage of these two terms that I suggest is most consistent with their generally understood meanings, although it rejects the precedent set by mycorrhizasts' common usage.

Host responsiveness to mycorrhizas

I use "responsiveness" to refer to the vertical magnitude of the effects of mycorrhizas on plant growth referenced to particular phosphorus availabilities. It may be positive, null, or negative as depicted by Fig. 3, and can be referred to as "mycorrhiza advantage" and "mycorrhiza disadvantage" when positive or negative, respectively. Responsiveness varies with fungus species (see Bever et al. 2002), experiment duration (which usually includes the effects of host developmental stage), and possibly with inoculum potential (Daft and Nicolson 1969; Ortaš 1996).

Absolute responsiveness can be measured as the difference in plant size (dry weight, or a morphometric measure; $W_m - W_{nc}$) between mycorrhizal plants (W_m) and non-colonized plants (W_{nc}) at a particular phosphorus availability. Usually, however, what I call "responsiveness" is relativized through division by either W_{nc} or W_m and is expressed as a percentage (Table 1). When expressed relative to the growth of plants with mycorrhizas ($W_m - W_{nc}/W_m$; e.g., Plenchette et al. 1983; Adjoud et al. 1996), it focuses on the non-colonized plants. It then represents the proportion of the size of mycorrhizal plants attained by plants without mycorrhizas. When relativized by the growth of plants without mycorrhizas ($W_m - W_{nc}/W_{nc}$; e.g., Estrada-Luna et al. 2000; Egerton-Warburton and Allen 2001), it reflects the proportional growth improvement attributable to mycorrhizas. When expressed as a percent, the latter index always is 100% less than the index of Menge et al. (1978; Table 1). The use of relative versus absolute responsiveness is analogous to the usage of tissue mineral element concentration versus content, or relative versus absolute growth rates. Each conveys different information. Concerning growth rates, for example, Koide (1991) states, "as far as phosphorus demand and its relation to phosphorus supply is concerned, it is absolute growth rate rather than relative growth rate that is of interest." Similarly, sometimes the absolute growth improvement attributable to mycorrhizas is of interest. As already noted, vertical calculations of responsiveness usually are made at a single level of phosphorus availability, but one could use the area between the phosphorus response curves of mycorrhizal and non-colonized plants for the range of phosphorus values over which mycorrhizas are advantageous (Fig. 3c) to reflect integrated positive responsiveness to mycorrhizas (Janos 1988).

Null responsiveness (the two intersection points of the phosphorus response curves of plants with and without mycorrhizas) indicates no net effect of mycorrhizas, not "no effect" (see especially Smith et al. 2003, 2004). Mycorrhizal fungi can impose a carbon cost upon their host by acting as a sink for photosynthate (Fitter 1991). When host responsiveness is null, the benefits of mycorrhizas exactly balance the cost. This may occur when phosphorus availability is so low that after meeting their own metabolic needs for phosphorus, mycorrhizal fungi supply just enough to the host to compensate what may be a proportionally high carbon cost. Their relative cost is likely to be high because the host's photosynthesis rate may be restricted by its limited phosphorus supply (see Harris and Paul 1987; Pearson and Jakobsen 1993). When phosphorus is abundantly available to a facultatively mycotrophic host (at the high intersection point in Fig. 3c), host growth is more likely to be carbon-limited than nutrient-limited, and so, again, the cost of mycorrhizas offsets their diminished benefit.

Comparing responsiveness to mycorrhizas among different host species at a single level of phosphorus availability potentially is misleading if the intent is to compare different host species' intrinsic capacities to respond to a mycorrhizal fungus or to a suite of fungi. A single phosphorus level is likely to represent relatively different positions on different plant species' phosphorus response curves. It would be best to compare the same relative position among plant species' curves, for example R_{max}—the maximum positive difference between the phosphorus response curves of plants with and without mycorrhizas. R_{max} of different plant species is not likely to occur at the same level of phosphorus availability.

Fungus effectiveness

However quantified, what I have called "host plant responsiveness" to mycorrhizas is the exact equivalent of the "effectiveness" of a mycorrhizal fungus or fungi in enhancing plant growth under a defined set of conditions. This is because our principal way of measuring fungus effectiveness is by host growth response. In an evolutionary ecological context, plant fitness improvement would be the best assessment of fungus effectiveness, but fitness is difficult to measure. The use of plant growth responsiveness to assess fungus effectiveness raises two caveats. The first is that when fungus effectiveness in association with different host species is compared, R_{max} (or a relativized variant of it) should be the measure employed. Otherwise, when considering a fixed level of phosphorus availability, one might conclude erroneously that a particular fungus species or a suite of several mycorrhizal fungi intrinsically stimulates the growth of one host species more than another. That may be taken prima facie as evidence of coevolution potentially leading towards specificity. On the contrary, it is possible that R_{max} values occurring within a natural range of phosphorus availabilities might not differ

(Fig. 5a,b), or a difference between host species $R_{\max}$ values might be the reverse of differences in responsiveness at a single level of phosphorus availability (Fig. 5c,d).

The second caveat is that at present, it may not be possible to compare the intrinsic physiological effectiveness of different mycorrhizal fungus species. Because we measure effectiveness by plant response, the time course of root colonization is inevitably confounded with the net benefits of a fungus to a host (Abbott and Robson 1984). Even if effort is made to equalize the inoculum potential of different fungus species so that they reach the same asymptotic level of colonization, then without repeated sampling of root colonization through time (such as that by McGonigle 2001) it is not possible to rule out colonization differences among fungus species before asymptotic colonization as a contributing factor (an example might be Lovelock and Miller 2002). Because young plants especially grow as if by "compound interest", a small advantage in early mycorrhizal colonization that enhances phosphorus uptake and photosynthesis may produce a large, persistent effect on plant growth. Conversely, the time required for mycorrhizal colonization to occur might render it impossible to precisely match total photosynthesis between fertilized, non-colonized and non-fertilized mycorrhizal plants (Eissenstat et al. 1993), thereby contributing to overestimation of the cost of mycorrhizas by comparison of mycorrhizal and non-colonized plants with similar phosphorus contents or concentrations (see Cooper 1984). Moreover, using host responsiveness as the measure of fungus effectiveness can tell us only net benefit, not gross benefit and cost. Pearson and Jakobsen (1993) tried to partially circumvent these difficulties by employing radioisotopes to directly measure short-term phosphorus transfer and carbon usage by hyphae. Dickson et al. (1999) related phosphorus supplied to the host, to the surface area of the host-fungus interface, and Smith et al. (2004) contrasted phosphorus supply to the host by *Arum*- versus *Paris*-type mycorrhizas. But we still do not know the intrinsic "exchange ratio"—how much phosphorus is provided to the host relative to the carbon received—for any mycorrhizal fungus (Jakobsen 1999).

Host dependence upon mycorrhizas

I use "dependence" to refer to the inability of a plant to grow without mycorrhizas below a particular level of soil phosphorus availability. That is, a plant species that can grow substantially without mycorrhizas at a lower level of phosphorus availability than another plant species is less dependent on mycorrhizas (≡more independent) than the other species. Although this presumes that any species that extensively forms mycorrhizas derives benefits from them (at least under some conditions), dependence of a mycotrophic plant species can be assessed with reference to the phosphorus response curve of only non-colonized plants. Thereby, dependence is a constitutive property of a plant species or genotype.

I suggest that dependence can be measured by the level of phosphorus availability below which there is little growth of plants lacking mycorrhizas. In practice, "little" growth can be defined as an arbitrary percentage of the growth asymptote (A) for plants without mycorrhizas. For example, in Figs. 2, 3, 4 and 5, I have calculated dependence (D) as 10% of the asymptotic non-colonized plant size according to the equation:

$$D = (-1/S) \times \ln\left(0.9AI/(0.1A(A-I))\right) \qquad (3)$$

Dependence, thereby, is measured in units of phosphorus, unlike responsiveness which is measured in units of a plant growth parameter. Accurate determination of dependence requires that sufficiently high levels of phosphorus be applied for the phosphorus response curve of plants without mycorrhizas to have closely converged upon its asymptote. Conversely, for plants grown in a soil that is so fertile as to have truncated the lower portion of the phosphorus response curve (e.g., Fig. 4d), the phosphorus fertilization level for 10% of asymptotic growth must be extrapolated and will be negative. This might be interpreted as, "how much soluble phosphorus must be removed from the soil to essentially prevent growth without mycorrhizas?" But extrapolation beyond the bounds of an experiment is perilous. Although a dependence value could be calculated from the phosphorus response curve of a species that never forms mycorrhizas (see Tester et al. 1988), I follow Menge et al. (1978) as defining species that are never mycotrophic as having no dependence.

In Fig. 3, I have refined my original model (Janos 1988) which I now believe to have been incorrect in three respects. In the original model, I did not represent the response of mycorrhizal plants at very low levels of phosphorus as the lower asymptote of a sigmoid curve. I postulated that minute additions of phosphorus would diminish the growth of mycorrhizal plants. After considering the physiology being modeled, I think that was incorrect. The second respect in which I find the original model (see Table 1) incorrect is that I thought plants with and without mycorrhizas would reach the same asymptote (there labeled T'), but I now appreciate that they may not (e.g., Fig. 4b,c). Accordingly, I have abandoned T'. The third respect in which the original model is incorrect is that I proposed that T' and a phosphorus threshold for growth without mycorrhizas (T, which essentially is equivalent to D as defined here) could be used interchangeably to produce the same rank order of plant species with respect to their dependence upon mycorrhizas. They would produce the same rank ordering only if the non-colonized plant phosphorus response curves of all plant species had very similar slopes (*S*). Otherwise, *T* and *T*′ could produce different plant species rank orders.

Siqueira and Saggin-Júnior (2001) examined the utility of my (Janos 1988) suggestion of using growth thresholds to rank species with respect to dependence on mycorrhizas. They concluded that *T*′ (as they calculated it), a continuous variable, was a better descriptor of the species they examined than Habte and Manjunath's (1991) dependency categories (see Table 1). Siquierra and Saggin-Júnior's *T*′, however, may not have measured dependence because they calculated it as the upper intersection point of phosphorus response curves for plants with and without mycorrhizas. When these curves do not have the same asymptote, their upper intersection point may not be highly correlated with *D* as calculated from only the phosphorus response curves of plants without mycorrhizas. Because they used plants both with and without mycorrhizas to calculate *T*′, Siqueira and Saggin-Júnior's (2001) values more likely represent aspects of responsiveness than dependence (as both are defined here).

Another potential problem with Siqueira and Saggin-Júnior's (2001) analysis is that they failed to find benefits of mycorrhizas for several large-seeded species that nevertheless demonstrated little ability to grow without mycorrhizas even with supplemental phosphorus. They categorized these species as independent of mycorrhizas, but their inability to grow without mycorrhizas suggests that these species are dependent. Perhaps Siquierra and Saggin-Júnior's experiments were too short (at 9 months or less), pots were too small, or the quantity and distribution of inoculum failed to produce adequate colonization (as suggested by their Table 2). The root systems of many tropical forest trees spread greatly and may bypass almost entirely a small quantity of inoculum placed in the planting hole, or they may become pot-bound such that seedlings are moribund. Similar problems may have confounded the results of Zangaro et al. (2000) for large-seeded tropical tree species.

As I already have noted, most published "mycorrhizal dependency" indices (Table 1) actually quantify what I suggest calling "responsiveness". Although dependence and responsiveness, as I have defined them, may be correlated, they need not be. Some of the debate surrounding Baylis' (1975) hypothesis that dependence is inversely correlated with root hair length and abundance may have been engendered by other authors' failure to distinguish between the phenomena of responsiveness and dependence. For example, seemingly in opposition to Baylis' (1975) hypothesis, Siqueira and Saggin-Júnior (2001) found a positive correlation between root hair length and the index of Plenchette et al. (1983), but I consider that an index of responsiveness. Perhaps an actual dependence measure (such as *D*) would support Baylis' hypothesis. Baylis (1975) states that the magnolioid root "...is the type of root most dependant upon conversion to a mycorrhiza for phosphorus uptake from the low levels of available P normally found in mature forest soils. For an uninfected plant to equal the growth rate of one that has mycorrhizas, sufficient soluble P has to be added to the soil to raise the Truog value 5–10 fold." Baylis (1975) seemed to infer "dependence" from the inability of plants without mycorrhizas to grow unless provided supplemental phosphorus, as I advocate here.

Facultative and obligate mycotrophism

Facultative and obligate mycotrophism as used by Janos (1980b) now can be defined with respect to non-colonized plant response to phosphorus availability. Both terms are intended to refer to a plant species' dependence on mycorrhizas, not to its responsiveness to them. Janos (1980b) defined facultatively mycotrophic plant species as those that can attain reproductive maturity without mycorrhizas at least in the most fertile of their natural habitats. Obligate mycotrophs are defined as those species that cannot grow or survive without mycorrhizas over the range of soil fertility that they naturally encounter (Janos 1980b). So, over the range of fertility of its natural soils, a *D* value could be determined for a facultatively mycotrophic species, but not for an obligately mycotrophic one. For an obligate mycotroph, *D* would exceed the highest phosphorus availability naturally encountered [e.g., Sieverding's Fig. 2.5a,b (Sieverding 1991)]. Fertilization in excess of the highest level of fertility encountered in its natural soils is necessary to quantify *D* of an obligately mycotrophic plant species. Although my conceptual model (Janos 1980b) of plant succession in relation to dependence on mycorrhizas was categorical and thereby discrete, in reality, facultative and obligate mycotrophs occupy a continuum of dependence. Along the entire continuum and within these two categories of mycotrophism, species can be ordered by their phosphorus thresholds for growth without mycorrhizas (*D*).

Trappe's (1987) effort [and similarly, Wang and Qui's (2006)] to categorize species as facultatively or obligately mycotrophic on the basis of whether or not they have been reported without mycorrhizas probably is imprecise. Trappe (1987) inferred correctly that if a species is encountered in a natural habitat as a reproductively mature adult without mycorrhizas, then that species is facultatively mycotrophic. A species encountered exclusively with mycorrhizas, however, cannot be assumed to be obligately mycotrophic because of the sparse and fragmentary nature of root colonization records. Only if in the most fertile of its natural soils it always has been found to be thoroughly colonized is its status likely to be inferred correctly from root examination. Beyond that, there is no reason to expect the colonized root length of field-collected plants to be strongly correlated with mycorrhiza dependence because colonization can vary seasonally (e.g., Torti et al. 1997), and a low percentage colonized root length might represent a high absolute number of mycorrhizas on a plant with a large root system (Gerdemann 1968).

Conclusions: how and why to adopt this conceptual model

My primary purpose in offering this model of plant responsiveness and dependence is to clarify the terminology. In addition, I hope that recognition of the different phenomena reflected by the terminology may provide new insight about the physiological function, ecological roles, and the evolution of mycorrhizas. My model has been developed in terms of plant phosphorus nutrition because phosphorus is the limiting mineral nutrient in many ecosystems, and much already is known about the effects of mycorrhizas on phosphorus acquisition by plants. In principle, the model might be applied to other mineral nutrients of which mycorrhizas enhance uptake when they are the element that limits growth. But, in practice, the predominant growth effects of mycorrhizas most often involve phosphorus (Smith and Read 1997). Also in principle, in an evolutionary context, the concept "dependence" should focus on the survival component of plant fitness, but that likely would require a field experiment with all mortality-producing factors present. It is difficult to maintain realistic control plants without mycorrhizas in the field. Hence, the principal value of my model is conceptual.

Notwithstanding its conceptual focus, this model can be applied to experiments with mycorrhizas and phosphorus supply that have certain salient characteristics. A substrate with very low intrinsic phosphorus ability must be used, such as acid-washed sand or a phosphorus-immobilizing soil in order not to truncate the phosphorus response curve of plants without mycorrhizas and return a negative D (Fig. 4d). Seven to nine or more levels of phosphorus availability should be produced. Many levels may allow minimal replication at each level while still providing reasonably tight confidence limits for fitted curve parameters. If the primary purpose of an experiment is to assess relative dependence (i.e., to estimate D) of plant species that are known to be mycotrophic, then only plants without mycorrhizas need to be grown. If mycotrophy must be demonstrated, then inoculated plants can be grown at a single, low level of phosphorus availability. If, however, either estimation of the phosphorus uptake value of mycorrhizas (a horizontal comparison) or determination of maximum responsiveness ($R_{\max}$) is desired, then full phosphorus response curves for both plants with and without mycorrhizas must be produced experimentally.

The model that I have proposed may be of conceptual value especially because it clarifies that natural selection can act directly on plant attributes that influence dependence, but natural selection is not likely to act directly on responsiveness. Dependence, as I have defined it, is likely a property of plant genotype, and so can be selected directly. Plant responsiveness and mycorrhizal fungus effectiveness, however, are properties that emerge from the interaction of independent plant and fungus genomes, and the evolutionary "best interests" of plants and mycorrhizal fungi may not always coincide (see Herre et al. 1999).

Application of this model also may aid understanding of the physiology and ecology of mycorrhizal plants. New questions emerge when one distinguishes between the phenomena of responsiveness and dependence. For example, the parameter S might be a more revealing index of plant phosphorus use efficiency than is the commonly calculated, static ratio of dry weight to phosphorus content (see Koide 1991). Furthermore, whether or not wild type progenitors have higher "dependency" (Tawaraya 2003) and lower phosphorus use efficiency than modern crop varieties (Zhu et al. 2001; Tawaraya 2003) perhaps should be investigated with respect to $R_{\max}$ and S. Do wild-type progenitors really have higher relativized $R_{\max}$ than cultivated varieties, or have the phosphorus response curves of cultivars without mycorrhizas simply been shifted to the left (i.e., lower D), thereby reducing the indices of Menge et al. (1978) and Plenchette et al. (1983) at a particular level of phosphorus availability while not changing $R_{\max}$ (e.g., Fig. 5a,b)? Finally, in an ecological context, can the often observed diminution of plant responsiveness to mycorrhizas with increased intraspecific competition (e.g., Schroeder and Janos 2004) be understood as a consequence of increased plant density shifting per capita phosphorus availability to the left [i.e., the reciprocal of plant density (=decreasing density) can be substituted for increasing soil solution phosphorus on the x-axis of Fig. 3c]? Coming to a full understanding of the role of mycorrhizas in plant competition, succession (e.g., Janos 1980b), and community composition (e.g., Urcelay and Diaz 2003) may necessitate acknowledging that responsiveness differs from dependence.

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