

# Influence of mycorrhizal strategy on the foliar traits of the plants on the Tibetan Plateau in response to precipitation and temperature

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Received: 26.04.2011

Accepted: 09.12.2011

**Abstract:** Mycorrhizas play key roles in important ecosystem processes and functions. To enhance our understanding of the impact of mycorrhizal strategies on important foliar traits of host plants and their response to climate changes, we analysed 6 selected foliar traits among 54 plant species in 129 sampling sites of ascertained mycorrhizal types on the Tibetan Plateau based on their functional groups. The selected traits were leaf mass per area (LMA), nitrogen concentration (on mass and area bases,  $N_{\text{mass}}$  and  $N_{\text{area}}$ , respectively), photosynthetic capacity ( $A_{\text{mass}}$  and  $A_{\text{area}}$ ) and photosynthetic nitrogen use efficiency (PNUE). The analysed foliar traits showed no significant difference between arbuscular mycorrhizas (AM) and non-mycorrhizas (NM) + AM in the grass group. Mycorrhizal strategies remarkably affected  $N_{\text{mass}}$  and  $A_{\text{mass}}$  of the herb group, and LMA,  $A_{\text{mass}}$  and  $N_{\text{mass}}$  in the shrub group. Responses of foliar traits to precipitation and temperature varied among different mycorrhizal strategies. The index of LMA,  $A_{\text{area}}$  and  $N_{\text{area}}$  of AM,  $N_{\text{area}}$  of NM/AM, and PNUE of mean annual precipitation (MAP) were significantly affected by mean annual temperature (MAT). The responses among different mycorrhizal types to precipitation and temperature differed among plant functional groups.

**Key words:** Mycorrhizal strategy, functional groups, foliar traits, precipitation, temperature

## Introduction

Vascular plant species acquire sufficient water, nutrients, and light to drive carbon fixation, and make enough carbon profit to ensure continuity to future generations (Wright et al., 2005). Leaf mass per area (LMA), nitrogen (N) concentration (on mass and area bases,  $N_{\text{mass}}$  and  $N_{\text{area}}$ , respectively), photosynthetic capacity (similarly,  $A_{\text{mass}}$  and  $A_{\text{area}}$ ), and photosynthetic nitrogen use efficiency (PNUE, defined

as photosynthetic capacity per unit leaf nitrogen) are fundamental foliar traits playing key roles in plant functioning (Schulze, 1994; Grime et al., 1997; Mooney et al., 1999; Ackerly, 2004). As a reflection of the dry-mass cost for producing new leaves, LMA correlates positively with leaf lifespan and negatively with leaf N concentration across species (Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004). Studies show that leaf N concentration is strongly correlated with photosynthetic capacity (Field & Mooney, 1986;

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Evans, 1989; Reich et al., 1994), as N is essential for the synthesis of Rubisco, the key enzyme of photosynthesis (Field & Mooney, 1986; Taiz & Zeiger, 1998). This correlation provides a useful link between processes on short-term leaf-level, and long-term plant- and stand-level, and has been used to estimate maximum CO<sub>2</sub> uptake over a broad range of species (Schulze, 1994; Baldocchi & Harley, 1995; Harley & Baldocchi, 1995; Aber et al., 1996; Williams et al., 1997; Larocque, 2002). Therefore, understanding the relationships between these fundamental traits and their large-scale patterns is essential for scaling up ecophysiological processes from the leaf level to the ecosystem level and in predicting ecosystem functioning in response to environmental change (Ehleringer & Field, 1993; Peterson et al., 1999; Norby & Luo, 2004). Over the past few decades, plant ecologists and physiologists have become increasingly concerned with quantifying correlations between key foliar traits (Arabaci et al., 2010; Güvenç et al., 2011; Mavi et al., 2011), and between foliar traits and climatic characters (Field & Mooney, 1986; Reich et al., 1992; Schulze, 1994; Körner, 1995; Grime et al., 1997; Reich et al., 1997; Niinemets, 2001; Wright & Westoby, 2002; He et al., 2006).

There is growing recognition that plant species and plant functional types are important controllers of ecosystem processes and functions (Hobbie, 1992; Chapin et al., 1997; Díaz & Cabido 1997; Grime et al., 1997; Tilman et al., 1997; Wardle et al., 1998), particularly those linking plants with the soils in which they grow (van Breemen, 1993; Berendse, 1994; Wardle et al., 1997; Cornelissen et al., 1999). At the same time, there is consensus that mycorrhizal symbioses between plants and soil fungi play some key roles in important ecosystem processes and functions (Grime et al., 1987; Fitter, 1990; Brundrett, 1991; Read, 1991; Rygiewicz & Andersen, 1994; Smith & Read, 2008; Heijden et al., 1998a, 1998b). We therefore expect that classifying plant species according to their mycorrhizal associations may provide a new dimension to research on functional type classification and application, from which, with few exceptions (Michelsen et al., 1996; Cornelissen et al., 2001), mycorrhizas have so far been excluded.

Mycorrhizal functional types should be based on the current understanding that different types of

mycorrhizal symbiosis, which also involve different fungal taxa, promote plant uptake of nutrients from different sources, notably nitrogen (N) versus phosphorus (P), inorganic versus organic forms (Read, 1991; Schulze, 1994; Chapin, 1995; Michelsen et al., 1998; Näsholm et al., 1998). In particular, the plant species that utilise complex organic N sources, as promoted by probably all ericoid mycorrhizal (Read, 1991; Kielland, 1994; Michelsen et al., 1996, 1998) and many or most of the ectomycorrhizal fungal associations (Read, 1991; Kielland, 1994; Northup et al., 1995; Michelsen et al., 1996, 1998; Näsholm et al., 1998) appear to contrast with plant species with arbuscular-mycorrhizal (AM) fungi, which generally have no access to complex organic nutrient sources. Instead, AM plants tend to take up inorganic P efficiently (Newsham et al., 1995; Heijden, 1998b; Smith & Read, 2008). It is thought that mycorrhizal symbioses could be central players in regulating leaf quality and plant growth rate (Pastor et al., 1984; Reich et al., 1992; Cornelissen et al., 1999; Aerts & Chapin, 2000). Cornelissen et al. (2001) analysed 83 British plants species of known functional and mycorrhizal categories and observed large variation in leaf parameters between mycorrhizal functional types. They claimed that plant species with ericoid mycorrhizas showed consistently lower inherent relative growth rate (RGR), lower foliar N and P concentrations, and poor litter decomposability, whilst ectomycorrhizal plant species had intermediate RGR, higher foliar N and P, and AM plants showed higher RGR, higher foliar N and P, and fast litter decomposition in contrast.

Different mycorrhizal types may have significant impact on important foliar traits (Smith & Read, 2008). However, mycorrhizal strategies are rarely noted when assessing the generality of foliar traits and their response to climate changes in large-scale patterns. The present study analysed 6 selected important foliar traits, i.e. LMA, N concentration ( $N_{\text{mass}}$  and  $N_{\text{area}}$ ), photosynthetic capacity (similarly,  $A_{\text{mass}}$  and  $A_{\text{area}}$ ), and PNUE, in comparison with their mycorrhizal strategies. The aim of this study was to determine the effect of different mycorrhizal functional types or mycorrhizal strategies of plants on their foliar traits, and to compare the response of foliar traits to precipitation and temperature based on mycorrhizal strategies.

**Materials and methods**

**Description of research area and sampling methods**

Sampling was carried out between late July and early August 2003 along a transect in the Central Tibetan Plateau. The transect covers latitudes from 28.19° to 36.32°N and longitudes from 86.83° to 100.93°E, and is approx. 2000 km long and 250 km wide. The sampling sites selected were subject to minimal grazing and other anthropogenic disturbances (He et al., 2006). At each site, the dominant plant species were collected at the flowering stage. A more detailed description can be found in He et al. (2006).

**Data compilation**

Data of foliar traits and site-specific precipitation and temperature for this study were drawn from the paper of He et al. (2006). The predominant mycorrhizal association of each species was classified according to the published literature and our observations (Harley & Harley, 1987a, 1987b, 1990; Wang & Qiu, 2006; Wang & Shi, 2008). The following 4 mycorrhizal

groups were classified according to the types of mycorrhizas associated with the studied host plants: (1) AM, plant species was colonised by arbuscular mycorrhizal (AM) fungi only; (2) NM+AM, plant species is non-mycorrhizal, or colonised by AM fungi; (3) Multi-mycorrhizas including ECM, plant was reported ever as ECM type, which represented ECM (shrub), ECM+AM (herb), and ECM+AM+NM (grass); (4) ericoid mycorrhizas (ERM) (Table 1).

The influences of mycorrhizal strategies on foliar traits were examined in 3 plant functional groups, i.e. grass, herb, and shrub (see He et al., 2006 for definitions).

The mycorrhizal strategies of 54 plant species in 129 plant sampling sites belonging to 35 genera and 20 families were ascertained and examined in this study (Table 1). Among them, 3 strategies (AM, NM+AM, and ECM+AM+NM) were included in grass, 4 (AM, NM+AM, and ECM+AM) in herbs, and another 4 types (AM, NM+AM, ECM, and ERM) in shrubs.

Table 1. Numbers of plant species, samples, genera, and families in each mycorrhizal type in 1 of the 3 plant functional groups.

Plant functional groups <sup>a)</sup>	Mycorrhizal functional types <sup>b)</sup>	Plant species/plant samples (sites)	Genera	Families
Grass	AM	10/32	6	2
	NM/AM	2/9	2	2
	ECM+AM+NM	1/1	1	1
Herb	AM	13/26	9	6
	NM/AM	10/21	9	7
	ECM/AM+ECM	1/4	1	1
Shrub	AM	11/23	8	5
	NM/AM	1/2	1	1
	ECM	3/8	1	1
	ERM	2/3	1	1
Total		54/129	35	20

<sup>a)</sup> Grass, including graminoids and sedges; Herb, including annuals, biennials and perennial forbs; Shrub, including deciduous shrubs and evergreen shrubs.

<sup>b)</sup> AM, arbuscular mycorrhiza; ECM ectomycorrhiza; EEM ectendomycorrhiza; NM/AM, nonmycorrhiza or arbuscular mycorrhiza; ECM+AM+NM, ectomycorrhiza, or arbuscular mycorrhiza, or nonmycorrhiza; ECM/AM+ECM, ectomycorrhiza, with or without arbuscular mycorrhiza; ERM, ericoid mycorrhiza; NM, nonmycorrhiza and mycoheterotrophy.

## Data analysis

The data were subjected to one-way analysis of variance using SPSS version 11.0 (SPSS, Chicago, IL, USA). All foliar traits were normalised by logarithm transformation prior to statistical analysis. Group means for the various foliar traits were compared by *t*-test for 2-group tests or by multiple comparison tests where more than 2 groups were compared by least significant difference (LSD) at the 5% or 1% level. Bivariate correlation analysis was performed to determine the correlation of foliar traits with mean annual precipitation (MAP) or mean annual temperature (MAT) in different mycorrhizal groups.

## Results

ANOVAs revealed that there were significant variations among different mycorrhizal strategy types for foliar LMA,  $A_{\text{area}}$ ,  $A_{\text{mass}}$ ,  $N_{\text{area}}$ , and  $N_{\text{mass}}$ . No significant difference in PNUE was observed with the change in mycorrhizal strategies (Table 2). Furthermore, the influence of mycorrhizal types on foliar traits was verified among different functional groups (Table 3). All foliar traits measured were not significantly different between AM and NM+AM in the grass group. As far as the herb group was concerned, mycorrhizal types affected leaf  $N_{\text{mass}}$  and  $A_{\text{mass}}$ , with no such effect on LMA,  $A_{\text{area}}$ ,  $N_{\text{area}}$ , or

Table 2. The effects of mycorrhizal strategies on foliar traits of plants on the Tibetan Plateau.

Mycorrhiza functional type	LMA	$A_{\text{area}}$	$A_{\text{mass}}$	$N_{\text{area}}$	$N_{\text{mass}}$	PNUE
AM	1.87 ± 0.015b <sup>a)</sup>	1.01 ± 0.023b	2.13 ± 0.021b	0.28 ± 0.014b	1.42 ± 0.012b	0.73 ± 0.022a
NM/AM	1.87 ± 0.024b	1.13 ± 0.026a	2.25 ± 0.030a	0.34 ± 0.028a	1.47 ± 0.021a	0.80 ± 0.020a
ECM/ECM+AM+NM	1.88 ± 0.024b	1.10 ± 0.051ab	2.23 ± 0.045ab	0.33 ± 0.027ab	1.47 ± 0.026a	0.77 ± 0.046a
ERM	2.14 ± 0.088a	0.96 ± 0.092c	1.81 ± 0.085c	0.29 ± 0.014ab	1.20 ± 0.055c	0.67 ± 0.016a

<sup>a)</sup>The number is average ± SE, different letters following the number mean significantly different at the 5% level.

Table 3. The effects of mycorrhizal strategies on foliar traits of plants in different functional groups on the Tibetan Plateau.

Plant functional groups	Mycorrhiza functional type	LMA	$A_{\text{area}}$	$A_{\text{mass}}$	$N_{\text{area}}$	$N_{\text{mass}}$	PNUE
Grass	AM	1.81 ± 0.017a <sup>a)</sup>	0.91 ± 0.044a	2.09 ± 0.040a	0.25 ± 0.021a	1.43 ± 0.014a	0.67 ± 0.040a
	NM+AM	1.88 ± 0.064a	1.04 ± 0.078a	2.17 ± 0.044a	0.31 ± 0.083a	1.43 ± 0.028a	0.78 ± 0.060a
	ECM+AM+NM	1.68	1.03	2.33	0.27	1.59	0.76
Herb	AM	1.87 ± 0.033a	1.09 ± 0.038a	2.19 ± 0.040b	0.30 ± 0.025a	1.43 ± 0.028b	0.79 ± 0.037a
	NM+AM	1.85 ± 0.024a	1.17 ± 0.021a	2.31 ± 0.029a	0.36 ± 0.023a	1.50 ± 0.025ab	0.81 ± 0.022a
	ECM+AM	1.81 ± 0.015a	1.06 ± 0.101a	2.24 ± 0.110b	0.33 ± 0.034a	1.51 ± 0.027a	0.73 ± 0.098a
Shrub	AM	1.92 ± 0.026b	1.05 ± 0.021a	2.12 ± 0.023ab	0.30 ± 0.030a	1.38 ± 0.021ab	0.76 ± 0.030a
	NM+AM	2.00 ± 0.032ab	0.94 ± 0.019a	1.93 ± 0.051c	0.24 ± 0.018a	1.24 ± 0.014bc	0.70 ± 0.037a
	ECM	1.90 ± 0.024b	1.13 ± 0.070a	2.21 ± 0.051a	0.35 ± 0.041a	1.44 ± 0.036a	0.79 ± 0.060a
	ERM	2.14 ± 0.088a	0.96 ± 0.092a	1.81 ± 0.085c	0.30 ± 0.014a	1.20 ± 0.055c	0.67 ± 0.087a

<sup>a)</sup>The number is average ± SE, different letters following the number mean significantly different at 5% level.

PNUE. In the shrub functional group, in contrast, mycorrhizal types had an impact on foliar LMA,  $A_{mass}$ , and  $N_{mass}$ , but no significant influence on  $A_{area}$ ,  $N_{area}$ , or PNUE.

The influence of mycorrhizal strategies on the responses of foliar traits to precipitations and temperature is given in Tables 4 and 5. Among all parameters, PNUE showed a negative correlation with MAP in the mycorrhizal type of ERM (Table 4). The index of LMA,  $A_{area}$  and  $N_{area}$  of AM,  $N_{area}$  of NM/AM, and PNUE of ERM were significantly affected by MAT, showing various correlations (Table 4). The response of different mycorrhizal types to MAP and

MAT varied among plant functional groups. In the grass group, significant influences of MAP and MAT on foliar traits were observed in AM rather than in the NM/AM group. MAP was not significantly correlated with any index in either the herb or shrub groups. A positive relationship was observed between LMA and  $A_{area}$  of the AM group, and  $N_{mass}$  of NM/AM and MAT, respectively (Table 5). When compared with the grass and herb groups, the shrub group showed a positive relationship between  $A_{area}$  and  $A_{mass}$  of the ECM group and MAT, but no significant correlation between any traits of the AM group and MAP or MAT (Table 5).

Table 4. Foliar traits in relation to mean annual precipitation (MAP) and mean annual temperature (MAT) in different mycorrhizal strategies.

Mycorrhiza functional type	LMA	$A_{area}$	$A_{mass}$	$N_{area}$	$N_{mass}$	PNUE
AM	-/+**a)	-/+*	-/+	-/+**	-/+	+/+
NM/AM	-/+	+/+	-/+	-/+*	-/+	-/-
ECM/ECM+AM	-/+	-/+	-/+	+/+	+/-	-/+
ERM	-/-	-/-	-/-	-/-	+/+	-*/-*

a) The minus (—) or the plus (+) symbol refers to the negative or positive relationship between foliar traits and MAP (in numerator position), or MAT (in denominator position), respectively.

\* and \*\* mean significant correlation at the 5% and 1% level, respectively.

Table 5. Foliar traits in relation to mean annual precipitation (MAP) and mean annual temperature (MAT) in different mycorrhizal strategies in each functional group.

Plant functional groups	Mycorrhizal functional type	LMA	$A_{area}$	$A_{mass}$	$N_{area}$	$N_{mass}$	PNUE
Grass	AM	-/+	-**/+	-*/-	-*/+*	-/+	-/-
	NM/AM	-/+	+/+	+/-	-/+	-/+	+/-
Herb	AM	-/+*	+/+*	-/+	-/+	+/-	-/+
	NM/AM	+/-	-/+	-/+	+/+	-/+*	-/+
	ECM/AM+ECM	+/-	-/+	-/+	+/-	+/+	-/+
Shrub	AM	-/+	-/+	+/+	-/+	-/+	+/-
	ECM	-/+	-/+**	-/+**	+/+	+/-	-/+

a) The minus (—) or the plus (+) symbol refers to the negative or positive relationship between foliar traits and MAP (in numerator position), or MAT (in denominator position), respectively.

\* and \*\* mean significant correlation at the 5% and 1% level, respectively.

## Discussion

The important function of mycorrhizal strategy in ecosystems has triggered interest in discussing further the effects of mycorrhizal association on ecosystems (Zhu & Miller, 2003; Vargas et al., 2010). It is well known that mycorrhizas influence nutrient cycling. Furthermore, the detailed mechanisms of mycorrhizal roles in nutrient cycling have partly been elucidated by major experimental efforts in mycorrhizal research. Previous studies have shown that mycorrhizal strategies influenced foliar traits such as foliar N and P (Cornelissen et al., 2001) and foliar  $d^{15}N$  (Craine et al., 2009) at ecosystem or biome level. Therefore, mycorrhizal symbiosis plays an important role in foliar traits.

Many researchers have shown that different mycorrhizal types involving different fungal taxa promote plant uptake of nutrients from different sources (Cornelissen et al., 2001). For example, ECM and ERM are suitable for stimulating plants to utilize complex organic N sources (Read, 1991), whilst AM plants tend to take up inorganic P efficiently (Smith & Read, 2008). Consequently, mycorrhizal types regulate plant growth rate and foliar nutrition properties differently (Cornelissen et al., 2001). Our results were consistent with previous observations indicating various impacts of different mycorrhizal types on foliar traits. LMA in the ERM group was higher than that in other groups due to the enhancement of ERM mycorrhizal type on plant LMA and the inherent high LMA in shrub species. Foliar  $A_{area}$ ,  $A_{mass}$ , and  $N_{mass}$  showed general agreement with the variation of mycorrhizal types, supporting the findings of Cornelissen et al. (2001). The possible reason for the low levels of  $A_{area}$ ,  $A_{mass}$ , and  $N_{mass}$  in the ERM group may be slow growing plant species with low nutrient concentration in the leaves (Cornelissen et al., 2001). In addition,  $N_{mass}$ ,  $N_{area}$ ,  $A_{area}$ , and  $A_{mass}$  in the NM/AM group had higher values than in the AM group. There may be connection with AM function that AM mostly contributed to the acquisition of P rather than N (Smith & Read, 2008). The  $A_{area}$  and  $A_{mass}$  in the NM/AM group were also high, which may be caused by high  $N_{area}$  or  $N_{mass}$  since N is closely related to photosynthetic capacity. However, each observed foliar trait was not significantly different between the ECM/ECM+AM+NM and AM groups,

or between the ECM/ECM+AM+NM and NM/AM groups. Furthermore, the values of  $N_{mass}$ ,  $N_{area}$ ,  $A_{area}$ , and  $A_{mass}$  in the AM group were lower than those in the NM/AM group. These results were in contrast to those of previous studies (Cornelissen et al., 2001; Parádi et al., 2003; Gamper et al., 2005; Baum et al., 2009). It is anticipated that some plant species in the NM/AM group could have developed mycorrhizal associations on the Tibetan Plateau and/or these plants could have other survival strategies under this particular ecosystem.

The influence of mycorrhizal types on foliar traits varied among plant functional groups. Mycorrhizal strategies did not significantly influence foliar traits in the functional group of grass. This result requires further investigation in terms of the small number of plant species sampled. High  $N_{mass}$  in the ECM+AM group among herbs may result from the difference of N uptake between ECM and AM (Read, 1991; Schulze, 1994; Chapin, 1995; Michelsen et al., 1998; Näsholm et al., 1998). This was also the case for the ECM group of shrub plants. The NM+AM group had the highest  $A_{mass}$ , confirming that the plant photosynthetic capacity was not correlated to leaf N concentration. Variation in inherent characteristics among plant species may explain the high LMA values observed for the ERM group among shrubs. Mycorrhizal strategy had no significant influence on N concentration, whether we analysed the data on an integrative scale or functional group scale. The N concentration could be sufficient so that there would be no limitation on the process of photosynthesis.

Previous studies analysed the influence of MAP or MAT on a number of foliar traits (He et al., 2006). To the best of our understanding, this study was the first attempt to compare the effects of MAP or MAT on foliar traits based on their mycorrhizal types. He et al. (2006) showed that the effect of MAT was significant for LMA,  $N_{area}$ , and  $A_{area}$ , but not for  $A_{mass}$  or  $N_{mass}$ ; the effect of MAP was not significant for any observed traits when mycorrhizal roles were ignored. That study, however, identified different patterns of influence of MAT or MAP on foliar traits when taking mycorrhizal associations into account (He et al., 2006). The significance of mycorrhizal roles on plant adaptive strategy is emphasised (Marjanovic et al., 2005; Mukhin & Betekhtina, 2006).

The finding of the different responses of foliar traits to precipitation and temperature related to mycorrhizal strategies enhances our understanding of plant responses to global climate changes and mycorrhizal ecology. The plant community or ecosystem would respond to climate changes differently when the role of mycorrhizas is concerned. Vargas et al. (2010) indicated that ecosystem CO<sub>2</sub> fluxes of vegetation types predominated by AM and ECM were differentially influenced by precipitation and temperature. Moreover, in terrestrial ecosystems, symbiotic associations between plant roots and mycorrhizal fungi are near ubiquitous, with 90% of all plant species forming mycorrhizas (Smith & Read, 2008). The symbiosis is well known with its function as an exchange of plant carbohydrate for fungal P; mycorrhizal colonization has also been shown to increase N acquisition (Perez-Moreno & Read, 2001) and improve the plant's resistance to drought and pathogen (Smith & Read, 2008). Clearly, considerable research effort is required in the future to allow

fully quantitative investigation of the function of mycorrhizal associations on a global ecosystem scale.

## Conclusion

Our results provide consistent support for the hypothesis that the mycorrhizal types play important roles in some foliar traits. The responses of foliar characteristics to precipitation and temperature varied under different mycorrhizal strategies.

## Acknowledgements

This study was financially supported by National Natural Science Foundation of China (Grant 40971150), and China Postdoctoral Science Foundation (20090450004, 20103018), the Science Foundation Fostering Innovative Ability (2009CZ0006), Scientific Research Fund (2007ZY06), and Doctoral Foundation (No. 06-34) of Henan University of Science and Technology.

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