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REGULAR ARTICLE

Stoichiometric mechanisms of *Dicranopteris dichotoma* growth and resistance to nutrient limitation in the Zhuxi watershed in the red soil hilly region of China

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Abstract
Aims Little is known about why *Dicranopteris dichotoma* can succeed in a nutrient-limited environment. This study investigated the stoichiometric mechanisms of *D. dichotoma* growth and resistance to nutrient limitation in the red soil hilly region of China.
Methods We examined *D. dichotoma* growth, soil nutrients, and stoichiometric variables in the early ecological restoration stage and across the ecological restoration chronosequence.
Results Most of the *D. dichotoma* growth factors rapidly increased with the arbor-bush-herb mixed plantation and maintained a high level. Soil P was a main factor influencing *D. dichotoma* growth across the ecological restoration chronosequence, whereas its role is unclear in the early ecological restoration stage. *D. dichotoma* demanded low C and P and possessed high N and P utilization rates, and N and P distribution was ranked as leaf>root and rhizome>stem. The stoichiometry of *D. dichotoma* is a relatively weak stoichiometric homeostasis across the whole ecological restoration chronosequence with relatively strong stoichiometric homeostasis in the early ecological restoration stage.
Conclusions Stoichiometry can be used to explore the underlying mechanisms that allow *D. dichotoma* to succeed to a great extent. *D. dichotoma* can play an important role in ecological restoration, and microtopography, especially valleys, should be created to trigger the succession of *D. dichotoma* in the red soil hilly region of China.

Keywords Ecological stoichiometry · Ecological restoration · *Dicranopteris dichotoma* · Red soil hilly region of China

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Introduction

The low vegetation cover, severe soil erosion, and poor soil fertility of a seriously degraded ecosystem may limit ecological processes in the early restoration stage (McCullough and Van Etten 2011). Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Bai et al. 2014), and measures need to be taken in time to induce progressive succession for ecosystem restoration in a short period of time. Ecological restoration measures can reduce soil and water loss, increase soil fertility, and improve ecological productivity (Wyant et al. 1995). By intervening in the earliest stage of succession, self-development can occur across the ecological restoration chronosequence by site preparation, vegetation plantation, and fertilization application. Herbaceous plants are one of the keys of ecological restoration, and the selection of suitable herbs has been carried out for decades to obtain improved restoration of sites (Zhu et al. 2011).

Ferns once dominated terrestrial plant communities across the entire globe and are still present in most terrestrial ecosystems (Lehmann et al. 2002). *Dicranopteris dichotoma*, a perennial fern of Gleicheniaceae (Wang et al. 2003), is one of the most widely distributed ferns throughout tropical to temperate regions. In more disturbed soils, only the hardiest, most resistant species can survive (Duan et al. 2009). We focused on *D. dichotoma* because it can grow in acidic soils (pH 4–5) and resist, tolerate, or thrive in very poor soils (Wang et al. 2003). Moreover, *D. dichotoma* dominates many plant communities and often forms pure patches; for example, the understory of *Pinus elliottii*, *Acacia crassicarpa*, *Eucalyptus urophylla*, and *Castanopsis hystrix*, which are widely planted in south China due to their fast growth and woody characteristics, is often occupied by dense *D. dichotoma* (Yang et al. 2014). These attributes single out *D. dichotoma*, whose presence can have significant impacts on the larger community- and ecosystem-level properties. Recent studies about *D. dichotoma* focused on growth in response to environmental factors (Li et al. 2013), materials and energy such as polysaccharides and antibiotic activities (Su 2005), net primary production and dynamics of carbon (Guan 2001), energy production, and the distribution of rare earth elements in *D. dichotoma* (Wang et al. 2006).

However, no scientific conclusion has yet been reached on long-term growth of *D. dichotoma*, the main influencing factors, and the underlying mechanisms that allow *D. dichotoma* to succeed. The study of short-term growth of *D. dichotoma* showed that it possessed morphological plasticity in different environments; for example, the height of *D. dichotoma* in infertile soil was 10–15 cm, while that in fertile soil was more than 1 m (Li et al. 2013). However, long-term observation of *D. dichotoma* growth is weak and insufficient. Previous studies have suggested that P is the most limiting element for growth and reproduction in natural ecosystems, while N seems to be relatively abundant (Du et al. 2011; González et al. 2011; Reed et al. 2011; Tischer et al. 2015). However, studies on the main influencing factors for *D. dichotoma* are still few and obscure. Limitation of P on *D. dichotoma* growth has been reported in eroded red soil region of south China (Li et al. 2013; Yue et al. 2014). To investigate the growth strategies and adaptability to extremely stressful conditions of *D. dichotoma*, a few studies analyzed the relationships between *D. dichotoma* and other plants using allelopathy; for example, the allelopathy of the extracts of the aboveground and underground parts of *D. dichotoma* inhibited the germination of the weeds including *Echinochloa crus-galli*, *Eleusine indica*, *Setaria viridis*, *Amaranthus spinosus*, *Alternanthera philoxeroides*, *Ambrosia artemisiifolia*, *Eclipta prostrate*, and *Xanthium sibiricum* (Luo et al. 1999). However, allelopathy cannot fully explain why *D. dichotoma* can succeed in a seriously degraded ecosystem.

Ecological stoichiometry, the study of the balance of multiple elements in ecological interactions and processes, suggests that it is not simply a limiting concentration of elements but the relationship between them that determines many important ecological processes (Elser et al. 2000; Wang and Moore 2014). It is well known that C, N, and P are the principal elements and the material basis of plants (Song et al. 2014a), and plant C, N, and P stoichiometry may significantly control the succession of vegetation (Song et al. 2014b; Lü et al. 2014). Stoichiometric homeostasis is a central concept in ecological stoichiometry representing the ability of organisms to maintain relatively constant conditions in the body despite fluctuations in the environment (Kooijman 1995; Yu et al. 2011). Stoichiometric homeostasis reflects underlying physiological and biochemical allocations as organisms respond to their surrounding environments, and thus, the degree of stoichiometric homeostasis may be highly relevant to fitness and to a plant species' ecological strategy (Yu et al. 2011). Little is known about the stoichiometry of *D. dichotoma*, despite the critical role of *D. dichotoma* in many tropical to temperate regions. To the best of our knowledge, this study may be the first to investigate the growth strategies and adaptability to extremely stressful conditions of *D. dichotoma* using stoichiometry.

The red soil hilly region of China lies between 32° N and 18° N, covering nine provinces and one autonomous region of southeastern China with a total area of 1.13 million km^2. The term "red soil" is not a single genus of soil but refers to well-drained red loams containing argillic, oxic, or plinthitic horizons and high contents of Fe and Al (Zou et al. 2009). Because of favorable hydrological conditions and high soil nutrient cycling capabilities, this region is important for the development of the county's agriculture and economic sectors (Cao and Zhang 1995). Historically, it was covered by luxuriant vegetation with light soil and water loss. However, a half century of human destruction increased the intensity and scale of soil and water loss, leading to heavy floods and droughts, degressive land productivity, and degraded ecological stability (Wang et al. 2011a). To obtain a better understanding of the underlying mechanisms that allow *D. dichotoma* to succeed in the red soil hilly region of China and to develop an effective ecological restoration, in this study, we analyzed the stoichiometric mechanisms of *D. dichotoma* growth and resistance to nutrient limitation in the early ecological restoration stage and across the ecological restoration chronosequence in the study area including the stands where the arbor-bush-herb mixed plantation (ABHMP) has been made and a stand without ecological restoration. Based on the above, we formulated the following four hypotheses: (1) *D. dichotoma* growth could be increased with ecological restoration across the ecological restoration chronosequence, (2) P was a main factor influencing *D. dichotoma* growth in the early ecological restoration stage and across the ecological restoration chronosequence, (3) the stoichiometric theory could potentially explain to a great extent the underlying mechanisms that allow *D. dichotoma* to succeed in the red soil hilly region of China, and (4) the stoichiometric homeostasis of *D. dichotoma* in the early ecological restoration stage was the same as that across the ecological restoration chronosequence. Answers to these questions may aid in the understanding of the complex effects of C, N, and P stoichiometry on *D. dichotoma*, and ultimately on ecological restoration in the red soil hilly region of China, and indeed in other similar regions worldwide.

Materials and methods

Study area

The most serious soil and water loss with the longest history and the largest area occurred in Changting County, southwest of Fujian Province in China (Bai et al. 2014; Zou et al. 2009). Covering a total area of 44.95 km^2, the Zhuxi watershed (116° 23′ 30″ to 116° 30′ 30″ E, 25° 38′ 15″ to 25° 42′ 55″ N), which is in the center of Changting County, represents the red soil hilly region in China. It was selected as one of 30 typical small watersheds by the Ministry of Water Resources in 2007, and the dynamic process of the soil and water loss was monitored. The landforms mainly consist of hills and low mountains. This region is affected deeply by a subtropical monsoon climate with warm and humid characteristics (the mean precipitation is 1730.4 mm/year, and the mean annual temperature is 18.3 °C) (Zou et al. 2009), the dominant vegetation cover (VC) is scattered Masson pine (*Pinus massoniana*), and the soil is derived from quaternary red clay and is classified as Argi-Udic Ferrosols (Chinese soil taxonomy) (Zhang et al. 2011). Historically, the Zhuxi watershed had good VC because of the high mean precipitation and warm annual temperature. However, for a long time, the over-exploitation already destroyed the balance of the ecosystem and turned this area into a typical ecological fragile zone (Bai et al. 2014; Zou et al. 2009).

Several ecological restoration measures have been made in recent decades, including ABHMP by the Soil and Water Conservation Bureau of Changting County, to restore a well-functioning ecosystem. The ABHMP planted trees, bushes, and herbs, such as *Schima superba*, *Liquidambar formosana*, *Lespedeza bicolor*, and *Paspalum wettsteinii*, in level trenches with Ca, Mg, and P compound fertilizer (about 900 kg/hm^2); the plants were then fertilized and tended for 3 years in the severe soil and water loss regions (Bai et al. 2014). One of the most obvious changes was the appearance and growth of *D. dichotoma* by itself after ABHMP.

Methods

Description of the study stands

The Soil and Water Conservation Bureau of Changting County has set up more than 100 typical long-term ecological research stands in recent decades. The experimental design involved six stands including a stand without ecological restoration (Laiyoukeng (LYK), grassland), a stand with natural forestry (Luhu (LH), broad-leaved forest), and four stands with ABHMP in October 2013. In this year, the years after restoration of the four stands with ABHMP were 2 (Duimountian (DM), established in 2011, shrub grassland), 7 (Longjing (LJ), established in 2006, coniferous forest), 13 (Youfang (YF), established in 2000, coniferous forest), and 30 (Bashilihe (BSLH), established in 1983, needle broad-leaved mixed forest). We considered LYK to be the early ecological restoration stage without ecological restoration. Like most chronosequence studies, this design was subject to pseudo-replication and space-for-time substitution limitations (Venterink et al. 2009). Nevertheless, the six stands were distributed on the same granite platform, with a homogeneous gentle slope in DM, LJ, YF BSLH, and LH and a variable slope in LYK. Therefore, we assumed that the ecological restoration time was the main factor contributing to change across stands.

Table 1 Classification criteria of microtopography in Laiyoukeng

Microtopography	Classification criteria
Ridge	TPI >0.4 SD
Upper slope	TPI >0.15 SD and ≤0.4 SD
Middle slope	TPI >−0.05 SD and 0.15 SD Slope >7°
Flat slope	TPI >−0.05 SD and ≤0.15 SD Slope ≤7 degrees
Lower slope	TPI >−0.3 SD and ≤−0.05 SD
Valley	TPI ≤−0.3 SD

SD standard deviation from elevation

D. dichotoma growth and *D. dichotoma* and soil samplings

For each stand, three standard representative plots (20× 20 m) were established and four subplots (1×1 m) were placed along a diagonal line of each plot. We estimated the VC of *D. dichotoma* by visual estimation in each subplot, and the averages were obtained as the VC of *D. dichotoma* in each plot.

A representative sampling point was selected in each plot in DM, LJ, YF, BSLH, and LH; that is, there were three representative sampling points in DM, LJ, YF, BSLH, and LH, respectively. The location was measured using a Trimble 5800 GPS (mean position accuracy=±0.1 m; 3358 points were measured) in LYK in August 2012. A high-resolution digital elevation model (DEM) with a cell size of 0.1×0.1 m was established using the measured points. We used both the Topographic Position Index (TPI) and the slope to form a microtopography layer including a six-class schema: valley, lower slope, flat slope, middle slope, upper slope, and ridge (Guisan et al. 2001) (Table 1, Fig. 1). The border of the *D. dichotoma* patches was measured using the same method and converted to ArcGIS to produce the *D. dichotoma* patch layer. The *D. dichotoma* patch layer and the microtopography layer were overlapped to calculate the area and percentage of different microtopographies in the *D. dichotoma* patches and to select the representative sampling points in LYK (Fig. 1). Based on the above class schema, three types of microtopographies (ridge, slope, and valley) along the microtopographic gradient were set in each plot in LYK. The slope included the lower slope, flat slope, middle slope, and upper slope, as they were narrow and limited for sampling. Thus, 27 representative sampling points (nine on the ridges, nine on the slopes, and nine on the valleys) were distinguished in LYK (Fig. 1).

A metal ring (diameter 35 cm) was placed in each sampling point for *D. dichotoma* growth and *D. dichotoma* and soil samplings. We measured *D. dichotoma* height (DDH) at five positions (one at the center and the other four from the circumference) within each ring, and five values were averaged to

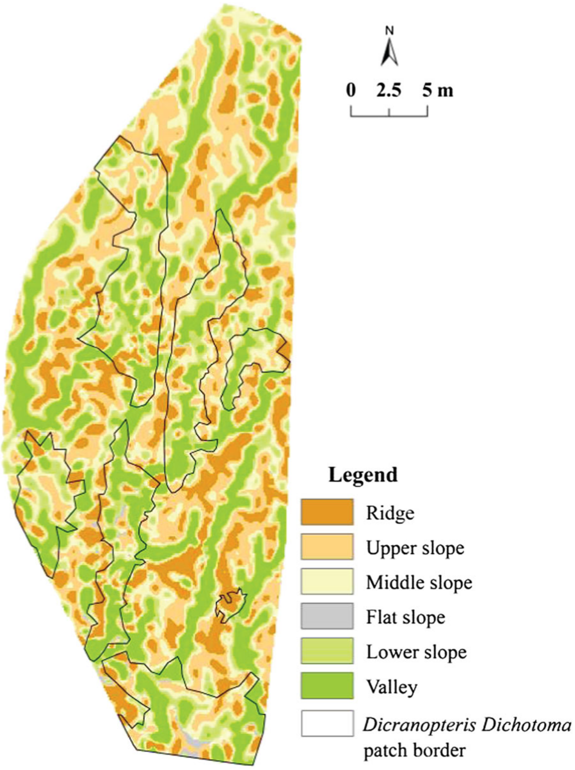

Fig. 1 Microtopographies and *Dicranopteris dichotoma* patches in Laiyoukeng

obtain one mean. The stem number of *D. dichotoma* within each ring was counted, and *D. dichotoma* density (DDD) was calculated. Given that *D. dichotoma* is a herbaceous plant, our analysis considered only measurements relative to the rooting zone (upper=20 cm of the soil profile). The aboveground standing biomass was harvested by clipping off all *D. dichotoma* at the soil surface, and belowground biomass was harvested by digging each ring to a depth of 20 cm. After collection, *D. dichotoma* were stored in polyethylene bags and shipped to the laboratory. Soil was sampled from the base of *D. dichotoma* to 20 cm below from the same ring used for *D. dichotoma* growth and *D. dichotoma* sampling. Soil was dug with a shovel at five positions (one at the center and the other four from the circumference) within each ring, and the soil was pooled into a composite sample and stored in polyethylene bags and shipped to the laboratory.

Measurements

D. dichotoma was rinsed with deionized water to remove dust and particles. The aboveground biomass was sorted into leaves and stems, and the underground biomass, which consists of roots and rhizomes, was not separated. We then separated *D. dichotoma* into leaves, stems, and roots and rhizomes. We dried the *D. dichotoma* tissues for 48 h at 80 °C and weighed them to determine the aboveground biomass per unit area (ABPUA), underground biomass per unit area (UBPUA), and total biomass per unit area (TBPUA). The dried *D. dichotoma* tissues were ground to fine powder prior to analysis. C and N in the tissues were measured with an elemental analyzer (Vario MAX CN; Germany), and P in the tissues was measured with a continuous-flow auto analyzer (Skalar SAN^{++}; Holland) after digestion of mixed solution of hydrofluoric acid and perchloric acid.

Visible roots, stones, and other debris were removed by hand from the soil samples prior to analysis, and the soil samples were then air-dried and sieved through a 2-mm nylon mesh. Soil C was measured using the method of oxidation with potassium dichromate in a heated oil bath, total N was measured by means of alkali distillation, and total P was measured by means of atomic absorption spectrophotometry. All of the cited soil analyses were standard and were performed according to the guidelines described by Liu (1996).

Statistical analysis

Data were collected in the fertilizing and tending period; thus, the data were used only for the analysis of *D. dichotoma* growth in DM. The averages of *D. dichotoma* growth, soil nutrients, and stoichiometric variables in each plot in LYK were obtained for comparison with the other stands, respectively. All our results for element concentration were expressed in grams per kilogram on a dry weight basis, and elemental ratios were converted to atomic ratios. Normality and homogeneity were verified using Kolmogorov-Smirnov's test and Levene's test, respectively, prior to analysis. When necessary, data were natural log transformed to meet the assumption of normality and homogeneity, but the raw (untransformed) data were reported in the tables (Han et al. 2014). One-way analysis of variance (ANOVA) with least square difference (LSD) was used to compare differences among *D. dichotoma* growth, soil nutrients, and plant stoichiometric variables, respectively. The relationships between plant stoichiometric variables and soil nutrients were assessed using Spearman's rank correlation analysis. Significance levels were set at P=0.05. All statistical analyses were performed using the SPSS software (version 19.0 for Windows; SPSS Inc., Chicago, IL, USA).

Results

D. dichotoma growth

Most of the *D. dichotoma* growth (DDH, DDD, ABPUA, UBPUA, TBPUA, and VC) showed significant differences in LYK, DM, LJ, YF, BSLH, and LH, respectively (P<0.05). DDH and DDD increased sharply then maintained a high level, and ABPUA, UBPUA, and TBPUA tended to increase across the ecological restoration chronosequence, respectively (Table 2), and VC increased from LYK to LJ and then decreased.

All *D. dichotoma* growth (DDH, DDD, ABPUA, UBPUA, TBPUA, and VC) showed significant differences among the three microtopographies (ridge, slope, and valley), respectively (P<0.05), and they tended to decrease in order from the valleys through the slopes to the ridges in LYK (Table 3).

The distribution of microtopographies in LYK and the *D. dichotoma* patches are provided in Table 4. We did not analyze the flat slope due to its small area percentage. The upper slope and valley were slightly

Table 2 *Dicranopteris dichotoma* growth, soil nutrients, and stoichiometric variables across the ecological restoration chronosequence

Variables	Stand					
	LYK	DM	LJ	YF	BSLH	LH
DDH (cm)	28.87±8.89 c	54.07±24.59 b	70.00±14.76 a	73.33±9.73 a	68.93±11.79 a	78.47±17.74 a
DDD (stem m^{-2})	367.43±57.27 c	769.53±464.24 a	433.29±130.02 b	523.42±75.23 b	477.16±162.10 b	513.02±168.11 b
ABPUA (g m^{-2})	0.87±0.16 c	1.26±0.17 b	2.06±0.23 b	2.48±0.23 b	2.83±0.23 a	2.89±0.29 a
UBPUA (g m^{-2})	0.20±0.06 c	0.35±0.03 b	0.40±0.10 b	0.51±0.04 b	0.59±0.04 b	0.61±0.07 a
TBPUA (g m^{-2})	1.08±0.16 c	1.61±0.14 b	2.46±0.15 b	2.99±0.20 b	3.42±0.19 a	3.50±0.36 a
VC (%)	24.00±23.28 c	79.83±23.84 a	88.08±12.24 a	84.67±24.25 a	67.33±30.22 b	16.27±23.09 c
Soil C (g kg^{-1})	6.62±0.80 b	–	7.93±1.28 ab	11.43±2.36 ab	15.77±1.71 a	16.61±4.87 a
Soil N (g kg^{-1})	0.47±0.04 b	–	0.50±0.09 b	0.61±0.12 ab	0.88±0.12 ab	1.14±0.30 a
Soil P (g kg^{-1})	0.09±0 c	–	0.10±0.01 bc	0.18±0.04 a	0.23±0.03 a	0.15±0.02 ab
Leaf C (g kg^{-1})	466.79±2.93 b	–	474.10±6.99 a	488.26±1.92 a	481.61±1.34 a	482.17±6.68 a
Stem C (g kg^{-1})	460.39±1.67 b	–	478.88±0.89 a	479.99±2.09 a	475.94±3.05 a	479.27±0.94 a
Root and rhizome C (g kg^{-1})	444.52±2.95 b	–	477.19±2.85 a	478.38±4.57 a	485.86±2.22 a	494.23±3.44 a
Leaf N (g kg^{-1})	8.76±0.33 c	–	9.54±0.34 bc	10.78±0.23 abc	12.29±0.64 ab	14.09±0.86 a
Stem N (g kg^{-1})	2.64±0.18	–	2.25±0.23	2.44±0.10	3.46±0.68	3.30±0.19
Root and rhizome N	3.29±0.17 b	–	3.66±0.16 ab	3.61±0.11 ab	5.30±0.98 a	5.24±0.54 a
Leaf P (g kg^{-1})	0.34±0.01 c	–	0.38±0.03 bc	0.43±0.04 abc	0.46±0.01 ab	0.54±0.04 a
Stem P (g kg^{-1})	0.08±0 b	–	0.11±0 ab	0.12±0.01 a	0.13±0.01 a	0.14±0.02 a
Root and rhizome P (g kg^{-1})	0.12±0.01	–	0.17±0.02	0.18±0.04	0.19±0.02	0.18±0.05
Leaf C:N	63.81±2.27 a	–	58.11±2.36 ab	52.88±1.31 abc	45.94±2.50 bc	40.28±3.12 c
Stem C:N	222.43±14.48	–	252.63±23.83	230.11±8.89	174.07±34.86	170.49±10.06
Root and rhizome C:N	166.22±8.76	–	152.51±5.56	155.00±5.80	115.83±24.49	112.03±10.35
Leaf C:P	3680.60±139.48 a	–	3241.31±268.59 ab	2975.79±235.72 ab	2688.44±83.15 ab	2330.16±176.56 b
Stem C:P	16,641.53±680.78 a	–	11,616.58±292.02 ab	10,121.22±581.89 b	9191.69±560.78 b	9487.33±1581.55 b
Root and rhizome C:P	10,923.83±785.73	–	7616.78±887.15	7592.67±1701.96	6680.93±576.83	7678.71±1610.80
Leaf N:P	58.62±2.52	–	55.74±3.72	56.50±5.77	58.74±2.63	57.91±2.26
Stem N:P	79.80±5.32	–	46.68±3.93	44.00±2.19	57.13±12.09	56.70±11.21
Root and rhizome N:P	68.45±5.66	–	50.06±6.10	48.42±9.14	60.68±7.34	67.84±11.92

Values followed by the same or no letters are not significantly different, and values followed by different letters are significantly different at $P<0.05$

more common in LYK. The *D. dichotoma* patches were found in all types of microtopographies, occurring in 30.09 % of the total area of LYK. The percentage of microtopographies increased in the *D. dichotoma* patches in the following order: ridge<upper slope<middle slope<lower slope<valley (Table 4).

Soil nutrients

Soil C, N, and P showed significant differences among LYK, LJ, YF, BSLH, and LH, respectively ($P<0.05$). Soil C, N, and P tended to increase across the ecological restoration chronosequence (Table 2).

Soil C and soil N showed significant differences among the three microtopographies (ridge, slope, and valley), respectively ($P<0.05$), while soil P was not significantly different among the three microtopographies (ridge, slope, and valley) in LYK. Soil C and soil N tended to decrease in order from the valleys through the slopes to the ridges, respectively (Table 3).

Relationships between *D. dichotoma* stoichiometric variables and soil nutrients

Part of the *D. dichotoma* stoichiometric variables (leaf C, stem C, root and rhizome C, leaf N, leaf P, stem P, leaf C:N,

Table 3 *Dicranopteris dichotoma* growth, soil nutrients, and stoichiometric variables among microtopographies (ridge, slope, and valley) in Laiyoukeng

Variables	Microtopography		
	Ridge	Slope	Valley
DDH (cm)	11.64±1.12 c	25.44±2.26 b	43.38±3.84 a
DDD (stem m^{-2})	117.56±16.10 c	345.30±40.95 b	560.11±55.98 a
ABPUA (g m^{-2})	110.28±18.50 c	434.35±61.55 b	1054.63±155.62 a
UBPUA (g m^{-2})	88.80±9.19 c	250.38±63.38 b	355.24±125.84 a
TBPUA (g m^{-2})	199.08±20.58 c	684.72±51.80 b	1409.86±260.67 a
VC (%)	15.79±1.33	22.45±1.87	34.65±3.02
Soil C (g kg^{-1})	2.09±0.08 b	5.71±0.78 ab	9.04±1.20 a
Soil N (g kg^{-1})	0.24±0.01 b	0.43±0.03 ab	0.58±0.06 a
Soil P (g kg^{-1})	0.09±0	0.09±0	0.09±0
Leaf C (g kg^{-1})	461.99±7.48	469.36±4.76	465.81±4.57
Stem C (g kg^{-1})	463.08±4.15	459.79±2.90	460.09±2.46
Root and rhizome C (g kg^{-1})	445.53±9.75	446.73±5.12	441.98±3.89
Leaf N (g kg^{-1})	7.03±0.47	9.12±0.46	8.97±0.50
Stem N (g kg^{-1})	2.74±0.14	2.74±0.32	2.50±0.29
Root and rhizome N (g kg^{-1})	4.16±0.34	3.07±0.24	3.22±0.23
Leaf P (g kg^{-1})	0.26±0.02 b	0.38±0.01 a	0.32±0.02 b
Stem P (g kg^{-1})	0.09±0.02	0.07±0	0.07±0.01
Root and rhizome P (g kg^{-1})	0.15±0.02	0.10±0.01	0.12±0.01
Leaf C:N	77.13±4.00	61.23±3.12	61.96±3.19
Stem C:N	197.42±8.12	216.42±23.00	236.78±25.14
Root and rhizome C:N	126.45±9.75	178.40±14.17	167.31±12.42
Leaf C:P	4543.31±409.23 a	3267.95±100.29 b	3805.67±187.68 ab
Stem C:P	14,277.70±2223.46	16,961.32±844.60	17,109.68±1142.45
Root and rhizome C:P	8043.58±1180.07	11,679.39±969.31	11,128.34±1457.22
Leaf N:P	59.62±8.18	54.38±3.00	62.53±4.26
Stem N:P	73.35±14.10	85.97±10.34	75.78±5.75
Root and rhizome N:P	65.53±14.43	69.88±9.35	68.00±9.04

Values followed by the same or no letters are not significantly different, and values followed by different letters are significantly different at $P<0.05$

leaf C:P, and stem C:P) was significantly correlated with soil C and soil N, respectively, and part of *D. dichotoma* stoichiometric variables (leaf C, stem C, root and rhizome C, leaf N, root and rhizome N, leaf P, stem P, root and rhizome P, leaf C:N, leaf C:P, stem C:P, root and rhizome C:P, and stem N:P) was significantly correlated with soil P, respectively, across the ecological restoration chronosequence (Table 5).

All of the *D. dichotoma* stoichiometric variables were not significantly correlated with soil nutrients in LYK (Table 6).

D. dichotoma stoichiometric variables

Part of the *D. dichotoma* stoichiometric variables (leaf C, stem C, root and rhizome C, leaf N, root and rhizome N, leaf P, stem P, leaf C:N, leaf C:P, and stem C:P) showed significant differences among LYK, LJ, YF, BSLH, and LH, respectively ($P<0.05$). Leaf C, stem C, root and rhizome C, leaf N, root and rhizome N, leaf P, and stem P tended to increase, respectively, while leaf C:N, leaf C:P, and stem C:P tended to decrease, respectively, across the ecological restoration chronosequence (Table 2).

All *D. dichotoma* stoichiometric variables were not significantly different among the three microtopographies (ridge, slope, and valley), respectively ($P<0.05$), except for leaf P and leaf C:P in LYK. Leaf P was ranked as slope>valley>ridge, and leaf C:P was ranked as slope< valley<ridge (Table 3).

Table 4 Areas and percentages of microtopographies in the *Dicranopteris dichotoma* patches and in Laiyoukeng

Microtopography	LYK		Patch	
	Area (m^2)	Percentage (%)	Area (m^2)	Percentage (%)
Ridge	101.63	14.41	19.91	9.38
Upper slope	182.40	25.86	39.37	18.55
Middle slope	139.28	19.75	41.67	19.63
Flat slope	3.83	0.54	2.75	1.30
Lower slope	122.85	17.42	48.19	22.71
Valley	155.38	22.03	60.35	28.43
Sum	705.37	100.00	212.24	100.00

Discussion

D. dichotoma growth

We formulated the first hypothesis that *D. dichotoma* growth can be increased with ecological restoration across the ecological restoration chronosequence, and DDH, DDD, ABPUA, UBPUA, and TBPUA supported the hypothesis, whereas VC did not. The soil was relatively poorer in all nutrients (C, N, and P), and DDH, DDD, ABPUA, UBPUA, TBPUA, and VC of *D. dichotoma* were significantly lower in LYK than in the other stands (Table 2). Sharp increases were observed in DDH, DDD, ABPUA, UBPUA, and TBPUA of *D. dichotoma* due to ABHMP in DM compared with LYK, suggesting that *D. dichotoma* growth rapidly increased with ecological restoration and maintained a high level. However, contrary to our first hypothesis, the VC of *D. dichotoma* increased from LYK to

Table 5 Correlation of *Dicranopteris dichotoma* stoichiometric variables with soil nutrients across the ecological restoration chronosequence

	Soil C	Soil N	Soil P
Leaf C	0.49**	0.50**	0.51**
Stem C	0.49**	0.43*	0.60**
Root and rhizome C	0.50**	0.48**	0.68**
Leaf N	0.60**	0.62**	0.59**
Stem N	0.21	0.27	0.11
Root and rhizome N	0.23	0.26	0.35*
Leaf P	0.42*	0.41*	0.52**
Stem P	0.39*	0.35*	0.47**
Root and rhizome P	0.12	0.07	0.49**
Leaf C:N	−0.59**	−0.61**	−0.53**
Stem C:N	−0.17	−0.23	−0.05
Root and rhizome C:N	−0.14	−0.19	−0.28
Leaf C:P	−0.39*	−0.38*	−0.52**
Stem C:P	−0.42*	−0.38*	−0.52**
Root and rhizome C:P	−0.03	0.01	−0.44*
Leaf N:P	0.27	0.32	0.10
Stem N:P	−0.20	−0.14	−0.37*
Root and rhizome N:P	0.17	0.23	−0.13

**$P<0.01$; *$P<0.05$; no symbol, $P>0.05$, significance of correlations

Table 6 Correlation of *Dicranopteris dichotoma* stoichiometric variables with soil nutrients in Laiyoukeng

	Soil C	Soil N	Soil P
Leaf C	0.11	0.15	0.03
Stem C	0.03	0.01	0.08
Root and rhizome C	0	0.02	0.30
Leaf N	0.30	0.31	0.17
Stem N	0.06	0.07	−0.17
Root and rhizome N	−0.14	−0.16	−0.03
Leaf P	0.05	0.05	0
Stem P	−0.14	−0.16	−0.38
Root and rhizome P	−0.35	−0.42	0.08
Leaf C:N	−0.30	−0.31	−0.15
Stem C:N	−0.06	−0.07	0.20
Root and rhizome C:N	0.18	0.21	0.05
Leaf C:P	0.02	0.03	−0.02
Stem C:P	0.09	0.11	0.26
Root and rhizome C:P	0.38	0.45*	−0.10
Leaf N:P	0.25	0.28	0.13
Stem N:P	0.11	0.13	0.12
Root and rhizome N:P	0.27	0.31	−0.03

*$P<0.05$; no symbol, $P>0.05$, significance of correlations

LJ and then decreased and VC in LH was even lower than that in LYK (Table 2). One possible explanation was that high VC of arbors and bushes under ABHMP hindered *D. dichotoma* growth in YF, BSLH, and LH as *D. dichotoma* are light-demanding heliophytes. However, VC of *D. dichotoma*, in general, was high in most of the ecological restoration stages.

Nutrient limitation in *D. dichotoma*

N:P in plant tissues, especially in leaves, has been studied intensively to determine how it limits plant growth (He et al. 2008). Several studies with different plant types, communities, and taxa have shown that N:P >16 indicates P limitation, N:P <14 indicates N limitation, and N:P between these values indicates N and P colimitation for plants (Pan et al. 2015; Koerselman and Meuleman 1996). Several other studies have shown that N is limiting when N:P is <10, and P is limiting when N:P is >20 (Sardans et al. 2012; Güsewell 2004). Although this approach is often criticized, it has been successfully applied to vascular plants (Wang and Moore 2014; Koerselman and Meuleman 1996). The leaf N:P of *D. dichotoma*, in a range of 55.74±3.72–62.53±4.26 (Tables 2 and 3), is higher than most of the N:P of different regions or plant communities (Table 7). According to the threshold values above, the leaf N:P of *D. dichotoma* was above 16 and 20, indicating that *D. dichotoma* is more P limited than N limited, although soil P increased across the ecological restoration chronosequence. Previous studies on diverse plant species have suggested that soil P is the most limiting element for growth and reproduction in natural ecosystems (González et al. 2011; Du et al. 2011) in subtropical and tropical regions. For example, a warm and wet subtropical and tropical climate enhances rock weathering and P mineralization and soil P becomes depleted with progressing pedogenesis (Campo and Gallardo 2012). According to recent studies, there may be a shortage of P in forest soils in China (Sun et al. 2012; Han et al. 2005). The forest soil P is 0.15–0.3 g kg^{-1} in the south subtropical zone in China, the average soil P is approximately 0.56 g kg^{-1} in China (Han et al. 2005), and the average global soil P is 2.8 g kg^{-1} (Reich and Oleksyn 2004). Soil P varied from 0.09±0 to 0.23±0.03 g kg^{-1} across the ecological restoration chronosequence and 0.09±0 g kg^{-1} in LYK, suggesting that soil P is much lower than that above due to severe soil and water loss in the red soil hilly region of China (Chen and Zhu 2006) (Tables 2 and 3). Thus, it is also suggested that *D. dichotoma* growth may be constrained by soil P. The N:P of *D. dichotoma* was not significantly different among LYK, LJ, YF, BSLH, and LH, suggesting that soil P is the main limiting factor in the early ecological restoration stage and across the ecological restoration chronosequence (Table 2).

Plants obtain most of their N and, practically, all of P from soil (Lerman et al. 2004). Generally, it is expected that increases in soil nutrients drive increased plant nutrient concentrations (Lü et al. 2014; Reed et al. 2011); for example, trees growing on more weathered and P-limited soils have lower leaf P (Campo and Gallardo 2012). Some studies suggested that significant correlations among plant traits with a soil nutrient implied that the soil nutrient is an important factor (Zhao et al. 2015); for example, the positive correlation between community biomass and soil inorganic N indicated that plants would be mainly N limited along a 30-year temperate steppe grazing exclusion chronosequence (Lü et al. 2014). We found that nearly half of the *D. dichotoma* stoichiometric variables changed with soil nutrients across the ecological restoration chronosequence. The number of the *D. dichotoma* stoichiometric variables significantly correlated with soil N was less than that of soil P, indicating that soil P was a more important factor than soil N across the ecological restoration chronosequence (Table 5). However, there was no relationship between the *D. dichotoma* stoichiometric variables and soil nutrients in LYK, indicating that soil nutrients were not dominant factors in the early ecological restoration stage (Table 6). This result was different from that originating from N:P, and it was difficult to explain but may be linked to the strategies that modify tissue nutrient concentration in a nutrient-limited environment (Bui and Henderson 2013; Lambers et al. 2010; Vitousek et al. 2010) in LYK. Different from our third hypothesis, soil P is a main factor influencing *D. dichotoma* growth across the ecological restoration chronosequence, while the effects of soil P on *D. dichotoma* and the mechanisms are in need of further study in the early ecological restoration stage.

Stoichiometric strategies of *D. dichotoma*

Nutrient limitation may impose severe constraints on the plants that reside there, and may favor plants with low nutrient demands (Lambers et al. 2010; Vitousek et al. 2010; von Oheimb et al. 2010). Thus, it is possible that a

Table 7 Leaf stoichiometric variables of different regions or plant communities

Region or plant communities	Representative species	C (g kg^{-1})	N (g kg^{-1})	P (g kg^{-1})	C:N	C:P	N:P	References
Globe	The terrestrial plant species	464	20.6	2.0	26.27	598.35	22.78	Elser et al. (2000)
The Loess Plateau in China		484	24.1	1.6	23.42	780.17	33.31	Zheng and Shangguan (2007)
Sub-alpine meadow	High-yield grass	530.5	19.9	2.2	31.09	621.91	20.00	Chen et al. (2013)
	Low-yield grass	525.1	22.8	1.9	26.86	712.78	26.54	
Temperate needle broad-leaved mixed forest	*Pinus koraiensis*	522.9	15.2	1.3	40.12	1037.39	25.86	Wang et al. (2011b)
	Fraxinus mandshurica	455.52	20.2	1.36	26.30	863.84	32.85	
	Tilia amurensis	484.9	25.6	2.33	22.09	536.74	24.30	
Tropical monsoon forest	*Garcinia cowa*	445.97	13.5	0.81	38.53	1419.99	36.86	Wang et al. (2011b)
	Barringtonia fusicarpa	490.35	19.98	1.3	28.62	972.81	33.99	
	Gironniera subaequalis	446.73	31	1.03	16.81	1118.60	66.56	
Subtropical evergreen broad-leaved forest	*Castanea henryi*	494.8	19	1.03	30.37	1238.96	40.79	Wang et al. (2011b)
	Cryptocarya concinna	548.6	20.2	1.15	31.67	1230.33	38.84	
	Aporusa yunnanensis	374.87	20.27	0.9	21.57	1074.25	49.81	
Subtropical plantation forest	*Pinus elliottii*	522.7	10.02	0.62	60.84	2174.33	35.74	Wang et al. (2011b)
	Cunninghamia lanceolata	510.65	10.88	0.75	54.74	1756.01	32.08	
	Pinus massoniana	522.59	14.77	1.02	41.26	1321.38	32.02	
	Schima superba	490.85	16.42	0.63	34.86	2009.43	57.64	

less nutrient demanding, larger species is able to survive in a greater range of locations (Lambers et al. 2010; Vitousek et al. 2010). The analysis of this study indicated that leaf C of *D. dichotoma* varied from 461.99±7.48 to 488.26±1.92 g kg^{-1} in the red soil hilly region of China (Table 2), in the range of leaf C of different regions or plant communities (Table 7). Leaf N of *D. dichotoma* varied from 7.03±0.47 to 14.09± 0.86 g kg^{-1} (Table 2), lower than most of leaf N of different regions or plant communities (Table 7). Leaf P of *D. dichotoma* varied from 0.26±0.02 to 0.54± 0.04 g kg^{-1} (Table 2), lower than all leaf P of different regions or plant communities (Table 7). It is suggested that *D. dichotoma* are rich in C but deficient in N and P in the red soil hilly region of China and demand lower N and P than many other plants. Leaf C, stem C, root and rhizome C, leaf N, root and rhizome N, leaf P, and stem P of *D. dichotoma* were significantly lower in LYK than those in LJ, YF, BSLH, and LH, suggesting that *D. dichotoma* demanded lower N and P in the early ecological restoration stage (Tables 2 and 3).

A recent study of ecological stoichiometry proposed that the plant growth status and corresponding metabolic conditions are reflected by C:N and C:P. Basically, C:N and C:P represent the ability of plants to assimilate C when simultaneously absorbing N and P (Song et al. 2014a). Under high N and P conditions, a higher growth and reproductive rate could be expected with lower C:N and C:P in the tissues, while under low N and P conditions, the efficiency in the use of resources is higher (Cuassolo et al. 2012), meaning that these types of plants fix more C per unit N and P (Reed et al. 2011). The analysis of this study indicated that the leaf C:N of *D. dichotoma* varied from 40.28±3.12 to 77.13±4.00 in the red soil hilly region of China (Tables 2 and 3), higher than most of the leaf C:N of different regions or plant communities (Table 7). The leaf C:P of *D. dichotoma* varied from 2330.16±176.56 to 4543.31±409.23 (Table 2), higher than all the leaf C:N of different regions or plant communities (Table 7). Leaf C:N, leaf C:P, and stem C:P of *D. dichotoma* were significantly higher in LYK than those in LJ, YF, BSLH, and LH, suggesting that *D. dichotoma* has a higher resource utilization rate in the early ecological restoration stage (Tables 2 and 3).

The plant's fitness depends, to a great extent, on resource allocation to different tissues (Leuzinger and Hättenschwiler 2013). By adapting to extremely low nutrient availability, some plants maintain small nutrient concentrations in photosynthetically active tissues (Wang and Moore 2014). However, *D. dichotoma* is different in the red soil hilly region of China. Leaf C, stem C, and root and rhizome C of *D. dichotoma* were not significantly different among LYK, LJ, YF, BSLH, and LH, respectively; leaf N, stem N, root and rhizome N, leaf P, stem P, and root and rhizome P showed significant differences among LYK, LJ, YF, BSLH, and LH, respectively ($P<0.05$) (Table 2). N and P distribution among different tissues was ranked as leaf>root and rhizome>stem, respectively (Table 2), and the same applied to LYK (Table 3). One possible explanation is that limited nutrients cause *D. dichotoma* to compete with other plants for nutrient acquisition by boosting the efficiency of light use. *D. dichotoma* must consume more N and P to construct leaves that increase light capture and photosynthesis (Pan et al. 2015), and the higher leaf N and leaf P are indicative of higher capture of light resources (Tischer et al. 2015).

A meta-analysis with 132 datasets from the literature has been conducted and revealed a wide range of stoichiometric homeostasis from strictly stoichiometric homeostasis to non-stoichiometric homeostasis (Persson et al. 2010). Weak stoichiometric homeostasis allows stoichiometric variables to vary with soil nutrients, which allows plants to work efficiently in a wide range of environmental conditions (Bui and Henderson 2013; Lambers et al. 2010; Sun et al. 2012; Vitousek et al. 2010). Strong stoichiometric homeostasis can keep their tissue stoichiometry stable, despite the changes of environmental conditions (Wang and Moore 2014). Strong stoichiometric homeostasis may be critical for species in arid and infertile environments, such as typical grassland (Yu et al. 2011). Because significant differences were observed in the stoichiometric variables, we can conclude that the stoichiometry of *D. dichotoma* exhibited relatively weak stoichiometric homeostasis across the ecological restoration chronosequence, while it exhibited relatively strong stoichiometric homeostasis in LYK (Tables 2 and 3). This suggests that different levels of stoichiometric homeostasis may evolve when more than one stage is involved in coping with nutrient deficiencies and nutrient changes. It is possible that relatively strong stoichiometric homeostasis of *D. dichotoma* in the early ecological restoration stage can explain less sensitivity to the nutrient-limited situation and a resistance to harsh conditions and relatively weak stoichiometric homeostasis of *D. dichotoma* across the ecological restoration chronosequence can indicate that *D. dichotoma* will modify C, N, and P with regard to the environmental conditions. This coupling of different levels of stoichiometric homeostasis may allow *D. dichotoma* to outperform other plants and be successful in a nutrient-limited environment (Naddafi et al. 2012). Thus, our third hypothesis was vindicated by the above analysis. Contrary to our fourth hypothesis, the stoichiometric homeostasis of *D. dichotoma* in the early ecological restoration stage is different from that across the ecological restoration chronosequence.

Implications for ecological restoration

The processes of development and succession in vegetation are slow in the red soil hilly region of China under natural conditions. Therefore, it is urgent to develop sustainable and economically efficient techniques for ecological restoration. *D. dichotoma* growth (DDH, DDD, ABPUA, UBPUA, TBPUA, and VC) can be increased with ecological restoration; then, DDH, DDD, ABPUA, UBPUA, and TBPUA can maintain a high level, and VC was high in most of the ecological restoration stages. Thus, *D. dichotoma* can possess a significant protective effect against soil and water loss by biomass and VC; moreover, *D. dichotoma* can self-develop after ABHMP ends 3 years later, which can significantly decrease costs related to the ecological restoration. Thus, *D. dichotoma* can maintain the structure and function of the plant community, improve soil nutrients, stabilize the ecosystem, and optimize the revegetation of the degraded ecosystem, endowing *D. dichotoma* with promising applications and a function as the "keystone genera" or "ecosystem engineer" in ecological restoration in the red soil hilly region of China. It may be a new way to realistically achieve the long-term objective of ecological restoration in the red soil hilly region of China using *D. dichotoma* as a basis for the control of soil and water loss and ecological restoration.

Microtopography of only a few centimeters is sufficient to affect ecosystem function by affecting an array of inter-connected physical, chemical, and biological variables. These findings have implications for many aspects of ecological restoration (Courtwright and Findlay 2011). For example, plots with mounds (artificial tussocks) using hands and shovels had twice as many species as plots without mounds in one bare restoration site in the wetlands (Peach 2005). Almost all of the *Sphagnum* recolonization was in the trenches of the drains on peatland in Quebec 30 years after abandonment (Price and Whitehead 2001). Although not legally mandated, microtopography is sometimes adopted as a performance/monitoring criterion in compensatory mitigation because it is understood to promote floral and faunal diversity. Thus, microtopography is sometimes intentionally induced during ecological restoration using a variety of techniques (Moser et al. 2007). *D. dichotoma* shows a greater area percentage on the valleys compared with the slopes and ridges in the *D. dichotoma* patches, and the dispersion of *D. dichotoma* is from valleys to ridges according to this study and our long-term observation in LYK. For this reason, valleys may be suitable for seedling establishment, plant growth, and community development. Thus, valleys have great potential in facilitating the dispersal of plants and enhancing soil fertility and in the effective ecological restoration of the degraded lands. Our results suggest that microtopography, especially valleys, should be created with a bulldozer or a hoe, if they are not present, in the red soil hilly region of China. Created microtopography has an important role in triggering the succession of *D. dichotoma* communities, thereby accelerating ecological restoration in the red soil hilly region of China.

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