Temperature Sensitivity and Basal Rate of Soil Respiration and Their Determinants in Temperate Forests of North China

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Abstract

The basal respiration rate at 10°C (R10) and the temperature sensitivity of soil respiration (Q10) are two premier parameters in predicting the instantaneous rate of soil respiration at a given temperature. However, the mechanisms underlying the spatial variations in R10 and Q10 are not quite clear. R10 and Q10 were calculated using an exponential function with measured soil respiration and soil temperature for 11 mixed conifer-broadleaved forest stands and nine broadleaved forest stands at a catchment scale. The mean values of R10 were 1.83 μmol CO2 m−2 s−1 and 2.01 μmol CO2 m−2 s−1, the mean values of Q10 were 3.40 and 3.79, respectively, for mixed and broadleaved forest types. Forest type did not influence the two model parameters, but determinants of R10 and Q10 varied between the two forest types. In mixed forest stands, R10 decreased greatly with the ratio of coniferous to broadleaved tree species; whereas it sharply increased with the soil temperature range and the variations in soil organic carbon (SOC) and soil total nitrogen (TN). Q10 was positively correlated with the spatial variances of herb-layer carbon stock and soil bulk density, and negatively with soil C/N ratio. In broadleaved forest stands, R10 was markedly affected by basal area and the variations in shrub carbon stock and soil phosphorus (P) content; the value of Q10 largely depended on soil pH and the variations of SOC and TN. 51% of variations in both R10 and Q10 can be accounted for jointly by five biophysical variables, of which the variation in soil bulk density played an overwhelming role in determining the amplitude of variations in soil basal respiration rates in temperate forests. Overall, it was concluded that soil respiration of temperate forests was largely dependent on soil physical properties when temperature kept quite low.

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Introduction

CO2 emission from soil and plants to the atmosphere determines the amplitude of feedbacks of forest ecosystems to global climate change. Accurate prediction of the amount of CO2 respired by forest soil is of great importance in evaluating the carbon balance of forest ecosystems. In most cases, soil respiration rate at a given temperature can be estimated by the empirical functions using soil basal respiration rate (R10), soil respiration rate at 10°C and the temperature sensitivity of soil respiration (Q10, a proportional change in soil respiration with a 10°C increase in temperature) [1,2,3]. Therefore, it seems vital to identify the biophysical variables driving these two parameters to advance the research on soil carbon turnover.

Soil respiration is mostly controlled by soil temperature [3,4], secondarily by soil moisture, nutrients [5], vegetation type [6], tree species composition [7], topography, and climate [8]. To increase the comparability of soil respiration rate under different environmental conditions, a standardized parameter (e.g. R10) is proposed when emphasizing the effects of biophysical factors other than temperature. Although soil basal respiration may also be influenced by the similar variables mentioned above [9], it is still of importance to make clear the relationship of soil basal respiration with biophysical variables in improving the precision of simulation models. This is because, for a specific forest ecosystem, some biophysical factors can be considered as additional predictive variables when estimating soil respiration rate using empirical methods [3,10].

Great effort has been exerted to the response of soil respiration to a change in temperature in recent decades [2,11], which is denoted in most studies to be the temperature sensitivity of soil respiration, and is theoretically represented by an invariant coefficient (Q10) of ~2, especially in coupled climate-carbon cycle models [12,13]. The extensive use of a fixed Q10 has brought large convenience in calculating the amount of CO2 respired from soil, but it has also evoked a controversy between theoretical studies and incubation experiments or field measurements [14]. It is demonstrated that the temperature sensitivity of soil respiration (Q10) can be influenced in ecosystems by many biophysical or physicochemical factors, including the forest floor conditions [15], soil physical properties [16], soil nutrients [17], and vegetation type [18]. Therefore, the Q10 originated from the temperature
dependence equation shows distinct intersite difference or temporal variation [16,17,19]. Obviously, the application of a constant $Q_{10}$ can not lead to an unbiased estimation of soil respiration rate for the studying ecosystem type any more.

Being illustrated by the calculation process of the common empirical function, an inherent correlation apparently exists between basal soil respiration and the temperature sensitivity [1,19]. Mathematically, $Q_{10}$ is dependent on, and acts as a multiplier of $R_{10}$ [19]. Any effort paid on the single parameter has limited use in improving the estimating precision of the extensively applied empirical functions.

Temperate forests in northern China mainly extend along the mountain ridge with heterogeneous growing conditions, which provide a natural experimental place for continuing similar research work on model parameters of soil respiration. In this study, we investigated the instantaneous rate of soil respiration and environmental variables at a representative catchment of the temperate forests in China, and calculated the two model parameters using the temperature dependent function. Herein hypotheses were proposed that the apparent temperature sensitivity of soil respiration could display detectable variations among forest types with different micro-environmental properties, and biophysical variables other than soil temperature could play an important role in determining soil basal respiration rate when the temperature decreased to a comparatively low level. Accordingly, our main objectives of this paper were to: 1) quantify the changing magnitude of model parameters of soil respiration within or between forest types; 2) identify the predominant variables controlling the spatial heterogeneity of the two parameters on the catchment scale in temperate forests.

**Materials and Methods**

**Ethics statement**

This research was conducted on field sites with the permission of the Taiyueshan Long-Term Forest Ecosystem Research Station. We declare that no privately owned land was used in this study, and that the field investigation did not involve any protected or endangered plant and animal species, and that no human or animal subjects were used in this study. The research has adhered to the legal requirements of China during the field study period.

**Study site and experimental layout**

This study was carried out at the catchment named after Xiaoshegou near the Taiyueshan Long-Term Forest Ecosystem Research Station (latitude 36°04′N, longitude 112°06′E; elevation 600 – 2600 m a.s.l.), which is about 190 km southwest of Taiyuan in Shanxi province of China. Annual mean temperature varies between 10°C and 11°C, with 26°C in the warmest month of July and -23°C in coldest month of January; whilst mean annual precipitation ranges from 300 mm to 600 mm [20]. The hill in the study area is at an elevation of 1800 m with its bottom of 1200 m a.s.l. The soil type of the hill slope belongs to a Eutric Cambisols (FAO classification) or a Cinnamon soil (Chinese classification) a.s.l. The soil type of the hill slope belongs to a Eutric Cambisols (FAO classification) or a Cinnamon soil (Chinese classification) a.s.l.

The herbaceous community is commonly composed of Carex lanceolata, Spodiopogon sibiricus, Rubia chinensis, Thalictrum petaloideum, Melica pappiana.

Twenty 20×20 m plots spread along four hill ridges with different topography at the small catchment, including 9 broad-leaved forest stands and 11 mixed conifer-broadleaved forest stands. The forest type was classified by the basal area ratio of coniferous to broadleaved tree species. The forest community was classified as the mixed forest type when its ratio fell within the range of 20% to 80%. Forest community structure was investigated in later Aug-2009. Each plot with diameter at breast height (DBH) >5 cm was measured for values of DBH and height respectively basing on tree species for these 20 plots. On each plot, five 5x5 m subplots were established for the investigation of shrub community, and five 1x1 m subplots for herbaceous community.

**Measurements of soil respiration**

Soil respiration rate was measured once per month for each forest stand during the growing season of May to November in 2008 and 2009, using a Li-Cor infrared gas analyzer (LI-8100, Li-Cor Inc., Lincoln, NE, U.S.A.) equipped with a portable chamber. The chamber was put on the top of installed collars for 2 minutes before measurements. In early April, nine polyvinyl chloride (PVC) collars were evenly placed on each plot with eight collars arranged in a circle at 5 m to the plot center and one right at the center. The PVC collar of 10 cm in diameter and 5 cm in height was permanently inserted 3 cm into the soil with 2 cm remaining above the surface of the forest floor. The live herbs or seedlings were carefully removed out the collars to avoid bias due to its respiratory activity just after plant growth occurred. Concurrently, soil temperature at 10 cm depth adjacent to each PVC collar was monitored using a thermocouple probe attached to LI-8100 system. The averaged data of soil respiration and soil temperature across the nine PVC collars per month were fitted to the following exponential model [1,10] to calculate basal parameters of soil respiration for each forest plot.

$$R_s = a \times e^{\beta T}$$

where $R_s$ is in situ soil respiration rate measured in the field, $a$ and $\beta$ are model parameters, $T$ is the measured soil temperature. According to equation (1), the temperature sensitivity of soil respiration was calculated by:

$$Q_{10} = e^{10\beta}$$

Soil basal respiration was calculated by:

$$R_{10} = a \times e^{10\beta}$$

**Measurements of environmental variables**

Shrub community was investigated by species for plant density and biomass of a representative sampling plant. The sampling plants were harvested and brought back to laboratory, and oven dried at 75°C to constant weight. The biomass of each shrub species within the community was estimated basing on plant density and its mean weight. The herbaceous plants in the 1 × 1 m subplot were all harvested for aboveground components. Additionally, litter on the forest floor was also collected in five 30×30 cm subplots on each plot. The herbaceous plant samples...
and litter were separately placed in envelope, transported to laboratory, and oven dried at 75°C for at least 48 h before weighing.

Soil cores of 4 cm in diameter and 20 cm in depth were sampled at five measurement positions on each plot in later growing season of 2009. The air dried soil samples were mounded to pass a 0.2 mm sieve for nutrient analysis after visible litter segments were picked out by hand. SOC and TN were determined separately following the modified Mehbie method [22] and the Kjeldahl digestion procedure [23]. Soil phosphorus (P) was measured using the colorimetric determination method described by John [24]. Soil pH was measured in deionized H2O using Sartorius AG (PB-10, Sartorius, Germany), after equilibration for 1 h in a water: soil ratio of 2.5:1. Soil cores were additionally excavated by a cylindrical sampler of 100 cm³ at five sampling positions on each plot, and oven dried at 110°C for at least 48 h in laboratory to measure the soil bulk density.

Data analyses

Soil physicochemical properties were also averaged for each plot when their effects on R10 and Q10 were analyzed. A two-tailed t-test was applied to detect the differences of R10 and Q10 between these two forest types at α=0.05. The spatial variability was expressed using the coefficient of variation (CV) calculated as the following.

\[ CV = \frac{SD}{M} \times 100\% \]  

where SD means standard deviation, and M represents mean value.

All these data analyses were carried out using the software of SSPPS 15.0. Figures were made using the software of SigmaPlot in version 10.0.

In order to test the combined contribution of biophysical variables to the variability of R10 and Q10, redundancy analysis (RDA) [25] was conducted with R10 and Q10 as dependent variables and with selected biophysical variables, i.e., DBH, soil pH, variances in soil bulk density, soil TN and soil pH, as explanatory variables. RDA was performed using the software of Canoco for Windows 4.5.

Results

Inter- and intra-forest-type variations in basal parameters

of soil respiration

R10 and Q10 were on average 10% and 11% higher in the broadleaved forest stands than in the mixed forest stands, although no statistically significant difference was detected between these two forest types (P=0.25 for R10 and 0.91 for Q10). There existed large spatial heterogeneity in temperature sensitivity and basal rate of soil respiration among forest stands. The CV of R10 ranged from 11% in the broadleaved forest to 19% in the mixed forest, and the CV of Q10 varied from 24% in the broadleaved forest to 29% in the mixed forests (Table 1).

Particularly, in the mixed forest stands, R10 was significantly affected by the basal area ratio between coniferous and broadleaved tree species, and greatly declined with the percentage of coniferous tree species. No significant correlation was found between Q10 and the basal area ratio in mixed forest stands (Fig. 1).

Determinant variables of soil basal respiration rate

R10 was mainly influenced by soil nutrient content and rose linearly with CV of SOC and CV of TN; soil temperature range during which soil respiration was monitored was significantly correlated with R10 in the mixed forest (Fig. 2A, 2B, and 3). Contrarily, in the broadleaved forest stands, R10 was largely determined by the basal area and the spatial variations of shrub carbon stock and soil phosphorus content (Fig. 2C and 4). There was a linearly inverse relationship between R10 and the basal area, whereas R10 increased differentially with increasing variations in shrub carbon stock and soil P in the broadleaved forest stands.

Determinant variables of the temperature sensitivity of soil respiration

In the mixed forest, Q10 was positively correlated with CV of herbaceous carbon stock and CV of soil bulk density (Fig. 5 and 6B), and negatively with soil C/N ratio (Fig. 7C). In the broadleaved forest, Q10 notably decreased with soil pH (Fig. 6A), but significant positive correlations were found between Q10 and CV of SOC and TN (Fig. 7A and B).

Combined relationships among R10, Q10 and biophysical factors

Although many environmental factors were found in this study to independently exert significant effects on individual parameter of R10 or Q10, 51% of the variations in both R10 and Q10 on the spatial scale were explained jointly by five biophysical variables, i.e., CV of soil bulk density, DBH, CV of soil TN, soil pH, and CV of soil pH, after forward selection of environmental variables. Particularly, most of the variations in R10 and Q10 were mainly ascribed to the variance of soil bulk density (Table 2). In addition, the importance of these selected factors was also highlighted by the result of Redundancy analysis, which showed that Axis 1 and Axis 2 accounted for 96.3% and 13.7% of the total variance in basal parameters of soil respiration, respectively (Fig. 8).

Discussion

Variation in R10 and its determining variables

Soil respiration rate at 10°C has received little attention in contrast to the instantaneous rate of soil respiration in the study of soil carbon cycle. Moreover, the comparability of R10 under changing circumstances is more reasonable than that of normally measured soil respiration rate. Even at the same temperature of 10°C, soil basal respiration still exhibits a large variation within or across forest types. On the scale of the catchment, R10 varies in a range of 1.25 μmol CO₂ m⁻² s⁻¹ to 2.30 μmol CO₂ m⁻² s⁻¹ in the mixed forest with a mean value of 1.83 μmol CO₂ m⁻² s⁻¹. R10 changes from 1.59 μmol CO₂ m⁻² s⁻¹ to 2.46 μmol CO₂ m⁻² s⁻¹ in the broadleaved forest with a mean rate of 2.01 μmol CO₂ m⁻² s⁻¹. These values of R10 just fall well in the range of R10 of different forests in the same region [3], but they are slightly higher than those for pine and oak forests in Brasschaat [26]. Given that the similar empirical function has been applied in calculating the basal rate of soil respiration, the variation of R10 is greatly induced by environmental factors other than soil temperature.

Stand structure has been indicated to be a dominant factor accounting for the spatial variation in soil respiration in beech and mixed-dipterocarp forests. Basal area and DBH exert a significant positive effect on soil respiration [4,27]. But, as to the specific results of this study, significant negative correlations are found between stand structure parameters and R10 for both forest types in the temperate region of North China. R10 declines differentially with the percentage of coniferous tree species in mixed forest community, and with the basal area across broadleaved forest stands. This intriguing scenario may be ascribed to the complexity...
of CO₂ production in forest soils. Soil respiration consists of autotrophic respiration from roots and rhizosphere and heterotrophic respiration from microbial decomposition. Total rate and basal rate of soil respiration have been found to be slightly higher in the pure broadleaved forest stands than in the pure coniferous forest stands [3]. R₁₀ is apparently depressed by the increasing admixed proportion of needle leaf tree species in the mixed forests. Perhaps, it is ascribed to the physiological differences between coniferous and broadleaved tree species. R₁₀ is indicated to be modulated by plant photosynthesis (i.e. gross primary productivity) [9] via determining the activity of rhizosphere respiration [20]. Autotrophic respiration accounts for 50% of total soil respiration, which may even be higher in growing season for temperate forests [29]. In cold weather with temperature at 10°C, photosynthetic activity of the mixed forest stands with higher basal area can be heavily impeded, subsequently resulting in a lower R₁₀.

Conversely, R₁₀ significantly increases with the heterogeneous properties of shrub carbon stock and soil P content in the broadleaved forest stands and by the spatial variations in soil organic carbon content and TN content in the mixed forest stands. This may be due to the dominance of microbial respiratory fraction in total soil respiration at lower temperature. It is the microbial community composition and climatic factors that control forest soil respiration in cold seasons [30]. Additionally, soil microbial biomass and respiration have been eventually influenced by soil biophysical properties [31] and by environmental biochemical processes [32] through substrate availability, which indicates that soil respiration is essentially an enzymatic controlled process [9,19].

**Variation in Q₁₀ and its determinants**

The temperature sensitivity of soil respiration, Q₁₀, shows evident intra- and inter-forest-type variations on the catchment scale in temperate forests of northern China. The average Q₁₀ values across forest stands for each forest type are larger than those of young plantations and a secondary *Populus davidiana* stand in the semiarid Loess Plateau [3]. However, the average Q₁₀ is comparable to the reported values by Peng et al. [18] and by Zheng et al. [17] through synthesizing a great number of studies about temperature sensitivity of soil respiration on the spatial scales from region to country. In essence, variant Q₁₀ values demonstrate the deficiency of the temperature dependent functions in describing the sensitivity of soil respiration to temperature.

The apparent Q₁₀ derived from field experiment is actually a combined temperature sensitivity of different fractions of soil CO₂ flux [10]. Particularly, the enzymatic reactivity of substrate decomposition to temperature is considered as the intrinsic Q₁₀ [19]. Although the Q₁₀ value of experimental study is suggested to be influenced by a wide range of ecological variables from molecular structure to climatic factors [18,19], the direct determinant of the temperature sensitivity of soil respiration is still dependent on the substrate availability [19]. In this study, we find that Q₁₀ could be markedly influenced by soil C/N ratio, soil pH, and the spatial heterogeneous properties of herbaceous carbon stock, SOC, soil TN, and soil bulk density. It is also worth mentioning that the contributors to the variations of Q₁₀ differ

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**Table 1. Variation in basal parameters of soil respiration within or between forest types.**

|          | R₁₀ (μmol CO₂ m⁻² s⁻¹) | CV of R₁₀ (%) | Q₁₀ | CV of Q₁₀ (%) |
|----------|------------------------|--------------|-----|---------------|
| Broadleaved forest | 2 a                    | 11           | 4 a | 24            |
| Mixed forest    | 1 a                    | 19           | 3 a | 29            |

The significance of differences of basal parameters between forest types were separately tested by independent t-test (two-tailed) at α = 0.05 (n = 9 in the broadleaved forest, and 11 in the mixed forest). Same lowercase letter means no significant difference is detected at α = 0.05 within 95% confidence interval between the two forest types.

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**Figure 1. Trends of R₁₀ and Q₁₀ with basal area ratio of coniferous to broadleaved tree species.**

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considerably between these two forest types. Similar results have been reported that the $Q_{10}$ values changed with the alteration of ecosystems and vegetation types [17,18]. Indeed, the extrinsic factors pose the effect on temperature sensitivity mainly via the primary control of substrate availability.

It has been recognized that the assumption of constant $Q_{10}$ of soil respiration is incorrect [9,16], because the sensitivity of soil respiration to temperature is a complex reactivity; also it is more than being described by a simple parameter of temperature-dependent models. To date, a consensus has not been reached to clarify the mechanism underpinning the temperature sensitivity of soil respiration, but the study of easily monitored variables, such as soil physicochemical properties, SOC, soil TN, and forest type, etc., will help add extra predictive factors other than temperature in interpreting the variability of the apparent $Q_{10}$.

The effects of forest types on the correlations between biophysical variables and $R_{10}$ and $Q_{10}$

$R_{10}$ and $Q_{10}$ have been demonstrated by our results to be influenced by biophysical factors and their spatial variation in forest stands. Although similar intrinsic mechanisms account for the variations of $R_{10}$ and $Q_{10}$ with forest microenvironments, the specific determining factors of soil basal respiration still vary with forest type. This is because forest type consisting of different tree species displays great distinctions in biotic and abiotic variables, which ultimately manipulate the changing gradient and direction of $R_{10}$ and $Q_{10}$.
At our study site, the mixed forest type is mainly composed of the coniferous tree species *P. tabuliformis* and the broadleaved tree species *Q. wutaishanica*. *P. tabuliformis* in forest ecosystem perhaps takes responsibility for the distinct correlations of $R_{10}$ and $Q_{10}$ with biophysical variables between broadleaved and mixed forest types, because tree species determines not only the microbial community structure but also the decomposition dynamics of forest litter [33,34]. Differences in the mycorrhizospheres and hyphospheres are the substantial way through which tree species affect soil microbial community including bacteria, archaea, fungi, and both free-living and symbiotic organisms [34]. Greater catabolic diversity and different bacterial and fungal communities have been found in the surface soil layer beneath mixed species plantations [35], and ectomycorrhizal fungi has been indicated to correlate with the presence of pine trees [36]. In addition, labile or soluble organic matter could also be affected by forest type with quantity and quality differences in litter and root exudates. This may induce the variations of soil microbial and enzyme activities between broadleaved and mixed forest types [37,38]. Obviously, the anisotropic response of heterotrophic respiration derived from microbial activity to biophysical factors may account for the variant correlations of $Q_{10}$ and $R_{10}$ with measured variables between the two forest types.

In general, $Q_{10}$ has a mathematical interrelationship with $R_{10}$ and they also can be expressed by each other [10]. Furthermore, both $Q_{10}$ and $R_{10}$ display the confounding reactions of the complex process of soil respiration to the changes in exterior environmental factors. Therefore it can improve the overall understanding of the underlying mechanism driving soil respiration to concurrently analyze the variances of $R_{10}$ and $Q_{10}$ and their determinants. Although a single variable can explain larger variance of $R_{10}$ or $Q_{10}$, the comparatively lower attribution of the

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**Figure 4. Correlations of $R_{10}$ with basal area and CV of shrub carbon stock separately for both forest types.**

**Figure 5. Relationships of $Q_{10}$ with variation of herbaceous carbon stock in both forest types.**
variation of $Q_{10}$ and $R_{10}$ to the five selected variables demonstrates the inherent interactions existing among biotic and abiotic variables. It is the internal interaction that determines the amplitudes of soil basal respiration rates with varying environmental conditions across temporal or spatial scales [10]. This viewpoint is also supported by the study of SOE and Buchmann [4]. Therefore, a more accurate estimation of soil CO$_2$ efflux cannot be achieved for a specific forest ecosystem until the changes in $Q_{10}$ and $R_{10}$ are concurrently taken into account with alterations of microenvironment.
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Author Contributions

Conceived and designed the experiments: ZZ, HM. Performed the experiments: ZZ, CG. Analyzed the data: ZZ. Contributed reagents/materials/analysis tools: ZZ, CG. Wrote the paper: ZZ.

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Table 2. The effects of biophysical variables on R10 and Q10 analyzed by the method of Redundancy Analysis (RDA).

| Variables          | Lambda-1 | Lambda-A | P   | F   |
|--------------------|----------|----------|-----|-----|
| CV of SBD          | 0.340    | 0.34     | 0.004 | 9.28 |
| DBH                | 0.244    | 0.07     | 0.152 | 2.01 |
| CV of soil TN      | 0.213    | 0.06     | 0.178 | 1.93 |
| Soil pH            | 0.204    | 0.03     | 0.454 | 0.81 |
| CV of pH           | 0.088    | 0.01     | 0.788 | 0.25 |

SBD: soil bulk density; DBH: diameter at breast height.

F: Describe marginal effects, which shows the variance when the variable is used as the only factor.

P: Describe conditional effects, which shows the additional variance each variable explains when it is included in the model.

Table 2 shows the level of significance corresponding to Lambda-A when performing Monte Carlo test (with 499 random permutations) at the 0.05 significance level.

Monte Carlo test statistics corresponding to Lambda-A at the 0.05 significance level.

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Figure 8. Redundancy analysis (RDA) among R10, Q10 and the biophysical variables. DBH means diameter at breast height; SBD means soil bulk density.

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|--------------------|----------|----------|-----|-----|
| CV of SBD          | 0.340    | 0.34     | 0.004 | 9.28 |
| DBH                | 0.244    | 0.07     | 0.152 | 2.01 |
| CV of soil TN      | 0.213    | 0.06     | 0.178 | 1.93 |
| Soil pH            | 0.204    | 0.03     | 0.454 | 0.81 |
| CV of pH           | 0.088    | 0.01     | 0.788 | 0.25 |

Q10, R10 and the Determinants in Temperate Forests

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