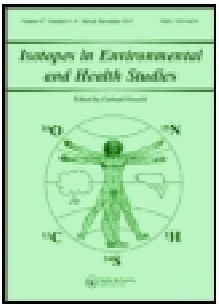

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Stable carbon and nitrogen isotope signatures of root-holoparasitic Cynomorium songaricum and its hosts at the Tibetan plateau and the surrounding Gobi desert in China

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Stable carbon and nitrogen isotope signatures of root-holoparasitic *Cynomorium songaricum* and its hosts at the Tibetan plateau and the surrounding Gobi desert in China

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We first measured the δ^{13}C and δ^{15}N values of root holoparasite *Cynomorium songaricum* and its hosts from 19 sites across four provinces in northwest China, in an attempt to investigate their nutritional relationship at the Tibetan plateau and the surrounding Gobi desert. Our study showed that the δ^{13}C of *C. songaricum* closely mirrored the values of its hosts, *Nitraria tangutorum* and *N. sibirica* across all sampling sites. *C. songaricum* was significantly depleted in ^{13}C compared to host plants at the Tibetan plateau, showing an average parasite/host δ^{13}C difference of -0.6 ‰. In contrast, ^{15}N of *C. songaricum* was significantly enriched by $+1.3$ ‰ compared to the hosts, implying that these holoparasites had other nitrogen resources. Although no difference in the δ^{13}C and δ^{15}N values between holoparasites and hosts was detected, the δ^{13}C and δ^{15}N values of holoparasites were significantly correlated with those of their hosts at the Gobi desert. The δ^{13}C versus δ^{15}N values were significantly but negatively correlated for the hosts; however, holoparasite/host variation in δ^{13}C was not correlated with the variation in δ^{15}N. The δ^{13}C versus δ^{15}N values were negatively correlated in *C. songaricum*, and this relationship tended to be magnified along the increasing elevations independent of the host plants. *C. songaricum* at the Tibetan plateau exhibited different δ^{13}C and δ^{15}N signatures compared with those at the Gobi desert. Furthermore, both δ^{13}C and δ^{15}N values of *C. songaricum* and its host plants in salt marshes at the Tibetan plateau were different from those in sand sites at the Tibetan plateau and the Gobi desert. Our results indicate that the isotopic difference depends on the different altitudes and habitats and is host-specific.

Keywords: arid area; carbon-13; Gobi desert; holoparasites; isotope ecology; nitrogen-15; nutritional relationship; plants; Tibetan plateau

1. Introduction

Parasitic plants can be classified as hemiparasites and holoparasites according to the extent to which they are unable to produce their own reduced carbon for growth and reproduction [1]. Unlike hemiparasites, holoparasites lack chlorophyll and are obligatory dependent on hosts for the organic and inorganic nutrition supplies through infecting both phloem and xylem of the hosts by the haustorium [2–4]. Although much literature has discussed the nutritional relationship of

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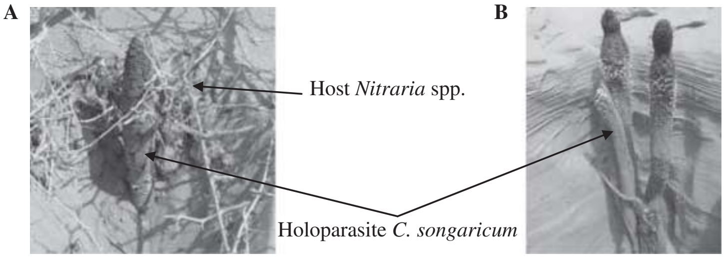

Figure 1. General features of the host plants *Nitraria spp*. and holoparasite *C. songaricum* at the Tibetan plateau and the surrounding Gobi desert. (a) Flowering *C. songaricum* below host plant *Nitraria* spp. (b) Immature *C. songaricum* parasitising deep roots of *Nitraria* spp.

holoparasites and their hosts in differing environments [2,5], there still exists little knowledge on the ecological interactions of the root holoparasites and hosts in arid areas [6,7]. The root holoparasite *Cynomorium songaricum* (Cynomoriaceae, Saxifragales), known in Chinese herbal medicine as 'suoyang', is widely distributed at the Tibetan plateau and the surrounding Gobi desert. *C. songaricum* produces swollen tuberous haustorial root connections to its host plants [8], mainly *Nitraria sibirica* and *N. tanguticum* (Nitrariaceae, Sapindales) (Figure 1). Occasionally, it is also found to parasitise the roots of other host plants such as *N. roborowskii*, *Zygophyllum xanthoxylum* and *Peganum harmala* [9]. Interest in these plants has increased in recent years, and they are being extensively collected from wild populations for use in herbal medicines, causing a dramatic decline of this herbal resource. The chemical components and therapy functions of *C. songaricum* have been studied in the past three decades [10–17]. However, the nutritional relationship of *C. songaricum* with its hosts has been little studied.

With the development of mass spectrometry, analyses of stable isotope ratios have been recognised as a powerful tool to investigate the carbon, water, and nutrient relations of parasitic plants and their hosts [18–26]. Stable carbon isotopes have been studied extensively to address various research questions and have provided valuable information about water use efficiency and carbon gain of parasitic plants [6,20,21,27]. However, identifying sources of nitrogen used by parasites needs further investigation [5]. Because holoparasites cannot produce reduced carbon through photosynthesis and other reduction processes, it has been suggested that identical or similar δ^{13}C values should be observed in the hosts and parasites [19,20]. However, a number of environmental factors, such as elevation, water availability, temperature and soil nutrition status, will have a strong influence on the stable isotope compositions of the hosts, especially for stable carbon isotopes [28–30]. Moreover, *C. songaricum* is often found to parasitise the deep roots of at least four water conservative host species distributed at the Tibetan plateau and the surrounding Gobi desert [9].

In this study, we analysed samples of *C. songaricum* and its hosts from 19 sites at the Tibetan plateau and the surrounding Gobi desert located at different elevations ranging from 1050 m to 3600 m in northwest China. We wished to investigate the nutritional relationship between *C. songaricum* and their hosts as well as the regional variations of this relationship among populations in different habitats (sand and salt marshes). We aimed to answer the question whether the patterns of stable isotopes in the holoparasite *C. songaricum* are identical along different environment gradients.

2. Materials and methods

2.1. *Study sites*

To examine the trophic strategies of *C. songaricum* from a wide geographic area of its natural range, samples were collected from 19 sites at the Tibetan plateau and the surrounding Gobi desert

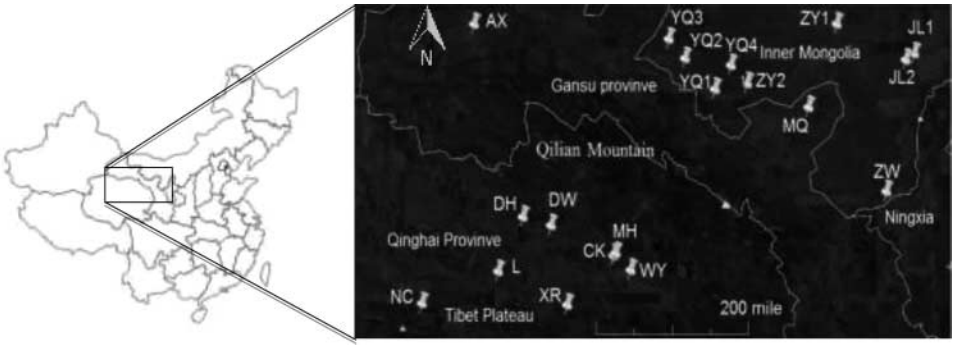

Figure 2. Map of sample collection across the Tibetan plateau and the surrounding Gobi desert. The characteristics of sites and IDs are listed in Table 1. Samples were collected from four provinces or autonomous regions: Qinghai province, Gansu province, Inner Mongolian autonomous region, and Ningxia Hui autonomous region.

in four provinces in northwest China. The selection of sampling sites was based on the presence of *C. songaricum*. Our sampling sites cover an area of 0.5 million km^2 (1000 km from west to east, and 500 km north to south) (Figure 2), and can be grouped into two distinct areas: (1) the Tibetan plateau with an average elevation of 3000 m, where *C. songaricum* mainly parasitises the roots of *Nitraria tangutorum*; (2) the surrounding Gobi desert with an average elevation of 1300 m, where *C. songaricum* is often found parasitising roots of *N. sibirica*. Both whole fleshy stems of *C. songaricum* and the attached roots of hosts were collected. Sampling sites and plant species collected are summarised in Table 1 and Figure 2. All samples were collected within a 20-d period in May 2010. Collection of *C. songaricum* fleshy stems and host roots was limited to an area of 1 ha at each site. Sample size (an individual of *C. songaricum* plus its attached hosts) at some sites was reduced due to extensive collection of *C. songaricum* by local residents.

2.2. *Analysis of stable carbon and nitrogen isotopes*

All samples were cleaned using distilled water and air-dried to constant weight in an oven at 70 °C for 48 h. They were separately ground finely and dispatched to an isotope ratio spectrometer for isotopic analysis using elemental analyser/continuous flow isotope ratio mass spectrometry as described by Bidartondo *et al.* [31]. Samples were analysed for N and C stable isotope abundances at the Laboratory of Stable Isotope Spectrometer, Chinese Academy of Forestry Sciences. The interface between the element analyser and the spectrometer was Flash EA1112 HT (Thermo Finnigan, USA). Operation conditions: oxidising furnace temperature was 900 °C, reducing furnace was 680 °C, pillar temperature was 40 °C. The resulting CO_2 and N_2 were purified in a vacuum line and injected in a Finnigan MAT Delta V advantage spectrometer (Thermo Fisher Scientific, Inc., USA) fitted with double inlet and collector systems. The results are expressed in $\delta^{13}C$ and $\delta^{15}N$ relative to the standards in the conventional δ per mil notation as follows:

$$\delta^{13}\mathrm{C} = \left[\frac{(^{13}\mathrm{C}/^{12}\mathrm{C})\ \text{sample}}{(^{13}\mathrm{C}/^{12}\mathrm{C})\ \text{standard}} - 1\right] \times 1000$$

$$\delta^{15}\mathrm{N} = \left[\frac{(^{15}\mathrm{N}/^{14}\mathrm{N})\ \text{sample}}{(^{15}\mathrm{N}/^{14}\mathrm{N})\ \text{standard}} - 1\right] \times 1000,$$

where $^{15}N/^{14}N$ are the isotopic ratios of sample and standard (atmospheric nitrogen); $^{13}C/^{12}C$ are the isotopic ratios of sample and PDB (Peedee Belemnite formation from South Carolina,

Table 1. Sampling sites of root holoparasite *C. songaricum* and its hosts (*Nitraria* spp.).

Area	Site ID	Latitude	Longitude	Elevation (m)	Habitat	Sample size (individuals)	Host plant	δ^{13}C (‰)	δ^{15}N (‰)
Gobi desert	JL1	39°39′59.52″N	105°49′40.68″E	1047	Sand	4	*N. sibirica*	−24.5 ± 1.4	5.3 ± 2.8
	JL2	39°34′42.72″N	105°37′13.80″E	1050	Sand	1	*N. sibirica*		
	ZW	40°10′52.50″N	104°3′36.72″E	1276	Sand	1	*N. sibirica*		
	MQ	38°56′40.92″N	103°20′11.10″E	1329	Sand	4	*N. sibirica*		
	AX	40°12′46.20″N	95°35′1.26″E	1342	Sand	1	*N. sibirica*		
	YQ4	39°36′43.98″N	101°35′52.50″E	1362	Sand	1	*N. sibirica*		
	YQ1	37°37′6.66″N	105°0′54.06″E	1362	Sand	4	*N. sibirica*		
	ZY1	40°10′52.50″N	104°3′36.72″E	1411	Sand	1	*N. sibirica*		
	ZY2	39°19′53.94″N	101°57′38.46″E	1420	Sand	1	*N. sibirica*		
	YQ2	39°43′48.06″N	100°33′3.12″E	1437	Sand	3	*N. sibirica*		
	YQ3	40°1′27.78″N	100°10′44.82″E	1438	Sand	1	*N. sibirica*		
Tibetan plateau	L	36°28′30.48″N	96°21′54.54″E	2760	Sand	4	*N. tangutorum*	−25.4 ± 0.9	8.9 ± 1.9
	DH	37°19′0.54″N	96°54′7.32″E	2817	Salt marsh	4	*N. tangutorum*		
	DW	37°12′17.00″N	97°32′37.00″E	2867	Salt marsh	3	*N. tangutorum*		
	CK	36°46′22.56″N	98°56′32.16″E	3073	Salt marsh	1	*N. tangutorum*		
	WY	36°33′30.06″N	99°19′34.32″E	3086	Sand	2	*N. tangutorum*		
	MH	36°48′38.12″N	98°59′42.52″E	3093	Salt marsh	4	*N. tangutorum*		
	XR	36°0′45.72″N	97°55′43.98″E	3108	Sand	2	*N. tangutorum*		
	NC	35°54′13.38″N	94°37′39.72″E	3623	Sand	2	*N. tangutorum*		

Notes: Sampling sites are ordered from low to high elevation, holoparasite–host species were pairs sampled at each site. δ^{13}C and δ^{15}N values are averages from host plants of the different sites.

USA) standard. The overall analytical precision was ±0.2 ‰ including both sample preparation and analysis.

2.3. *Statistical analysis*

Nonparametric Tests (Mann–Whitney *U*) were used to detect the differences in the δ^{13}C and δ^{15}N values in the holoparasites and hosts collected from different locations and the differences in the δ^{13}C and δ^{15}N values between the holoparasites and host plants. Spearman's rank correlation analysis was used to test the correlation between the δ^{13}C and δ^{15}N values of the holoparasites or host plants, the stable isotopic correlation between the holoparasites and host plants, as well as holoparasite/host variations in the δ^{13}C and δ^{15}N values.

3. Results

Our results showed that the average δ^{13}C values of the host plant *N. tangutorum* from the Tibetan plateau (-25.4 ± 0.9 ‰) were significantly lower than those of *N. sibirica* from the Gobi desert (-24.5 ± 1.4 ‰) (Nonparametric Mann–Whitney *U* test: $Z = -2.206$, $P = 0.027$) (Table 1).

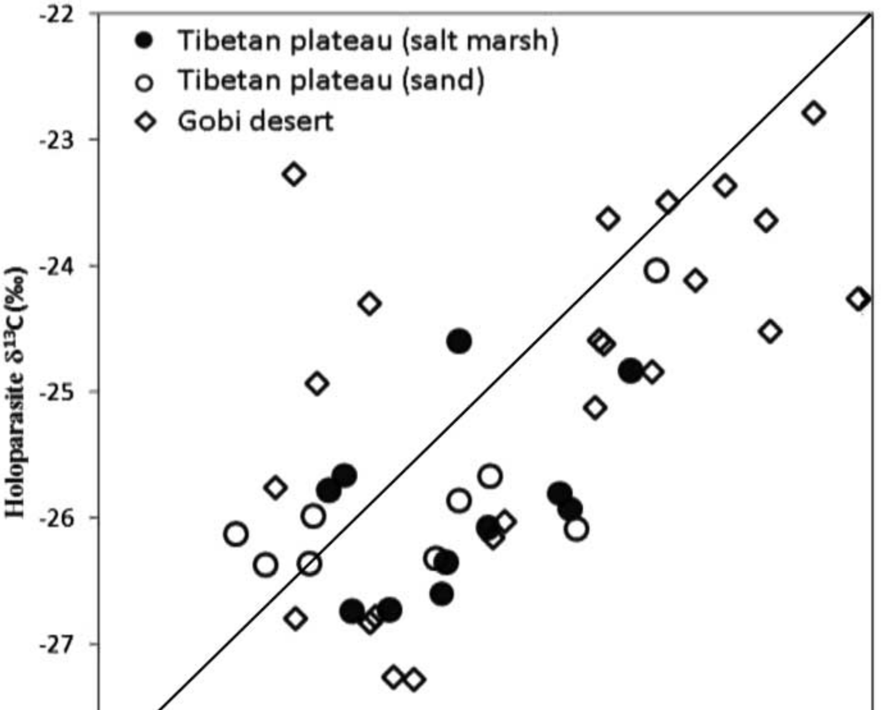

Figure 3. The δ^{13}C values of holoparasitic *C. songaricum* from the Tibetan plateau and the surrounding Gobi desert plotted against the root δ^{13}C values of its hosts. A one-to-one line is drawn for easier comparison. Sample sizes from the Tibetan plateau and the surrounding areas are both 22.

However, host plants from the Tibetan plateau exhibited higher δ^{15}N values compared with those of the Gobi desert (8.9 ± 1.9‰ versus 5.3 ± 2.8‰) ($Z = -3.943$, $P < 0.001$) (Table 1). Correspondingly, the δ^{13}C values of the holoparasite *C. songaricum* parasitising *N. tangutorum* were significantly more negative than those parasitising *N. sibirica* (-26.0 ± 0.8‰ versus -24.9 ± 1.4‰) (non-parametric T test: $Z = -2.723$, $P = 0.006$) (Figure 3), whereas the δ^{15}N values were significantly enriched compared to *C. songaricum* collected from the Gobi desert (10.1 ± 2.2‰ versus 6.5 ± 2.7‰) ($Z = -3.967$, $P < 0.001$) (Figure 4). A significant difference was found in the δ^{15}N but not for δ^{13}C values of *N. tangutorum* between sites on sand and salt marshes at the Tibetan plateau (δ^{13}C: $Z = -0.725$, $P = 0.468$; δ^{15}N: $Z = -2.110$, $P = 0.035$) (Figure 5). However, no difference was found in the δ^{13}C and δ^{15}N values of *C. songaricum* (δ^{13}C: $Z = -0.066$, $P = 0.947$; δ^{15}N: $Z = -1.055$, $P = 0.291$). A significant difference was found in the δ^{13}C and δ^{15}N values of the host plants from the sand habitats at the Tibetan plateau and the surrounding Gobi desert (δ^{13}C: $Z = -2.033$, $P = 0.042$; δ^{15}N: $Z = -2.480$, $P = 0.013$). Correspondingly, a significant difference was found in the δ^{13}C and δ^{15}N values of *C. songaricum* between the two sampling areas (δ^{13}C: $Z = -2.074$, $P = 0.038$; δ^{15}N: $Z = -2.683$, $P = 0.007$) (Figure 5).

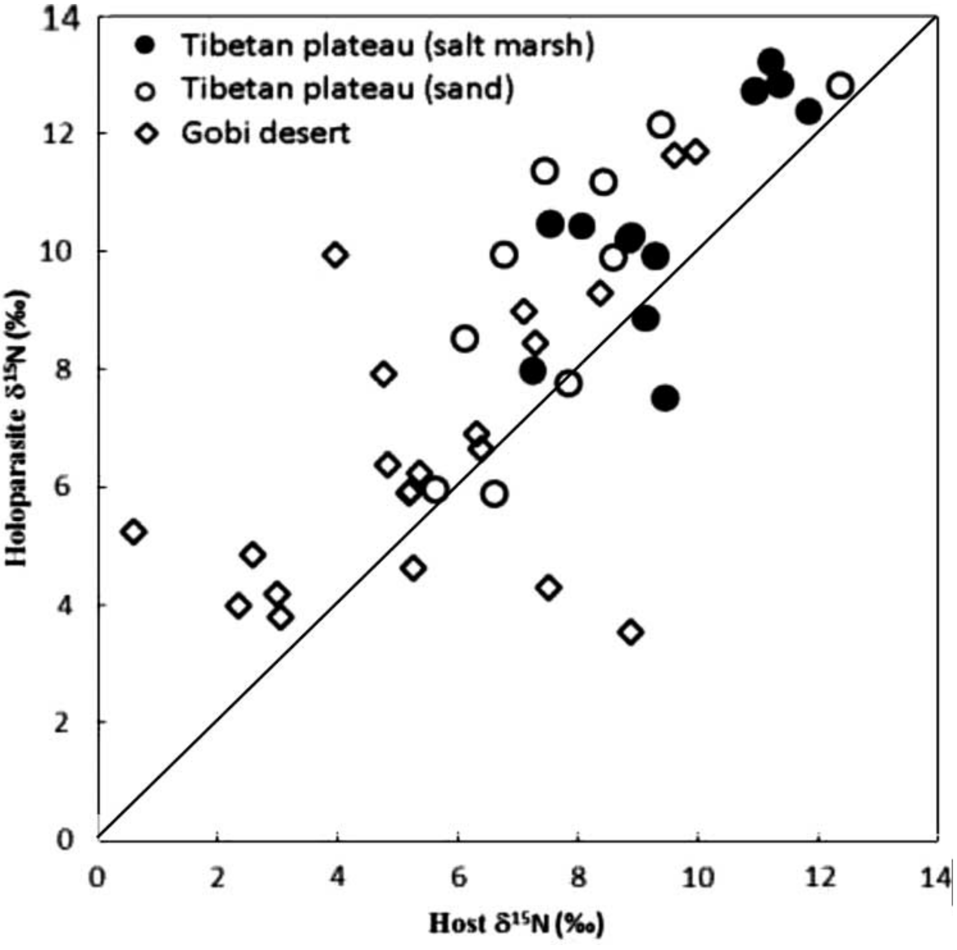

Figure 4. The δ^{15}N values of holoparasitic *C. songaricum* from the Tibetan plateau and the surrounding Gobi desert plotted against the root δ^{15}N values of its hosts. A one-to-one line is drawn for easier comparison.

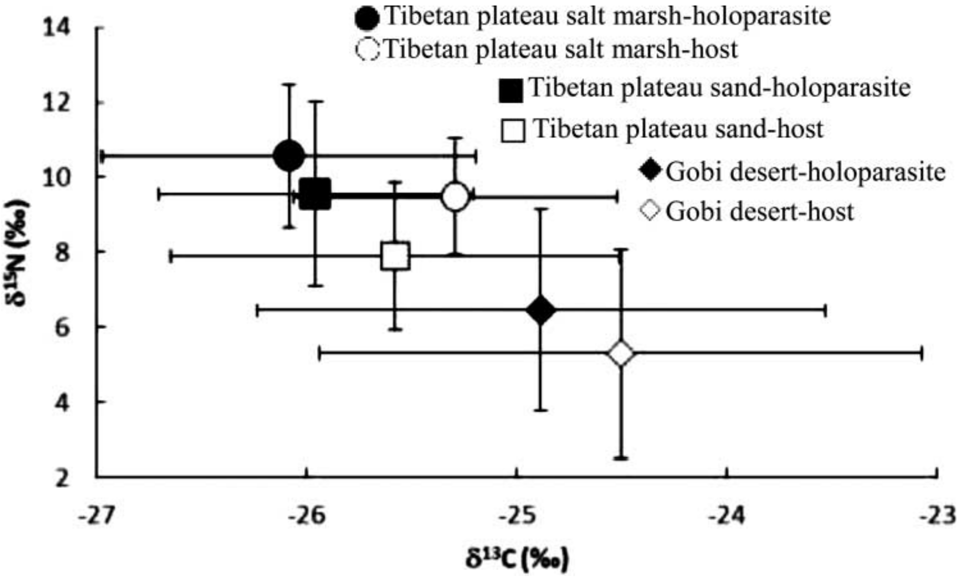

Figure 5. The overall difference (mean ± SD) in the δ^{13}C and δ^{15}N values of *C. songaricum* and its hosts in the Gobi desert sand, salt marshes, and sand habitats at the Tibetan plateau.

Our results also showed that the stable isotopic signatures of the holoparasite *C. songaricum* closely mirrored the values of its hosts *N. tangutorum* or *N. sibirica* across sampling sites (Figures 3 and 4). Root-holoparasitic *C. songaricum* was significantly depleted in ^{13}C compared to the host *N. tangutorum* at the Tibetan plateau ($Z = -2.136$, $P = 0.033$) (Figure 3), showing an average holoparasite/host δ^{13}C difference of −0.6 ‰ ($N = 22$, $P = 0.020$). In contrast, ^{15}N of *C. songaricum* was significantly enriched compared to its hosts ($Z = -2.136, P = 0.033$), with an average holoparasite/host δ^{15}N difference of +1.3 ‰ ($N = 22$, $P = 0.001$) (Figure 4). Although no significant enrichment of isotope signatures was found between the holoparasite and its hosts in the Gobi desert (δ^{13}C: $Z = -0.915, P = 0.360$; δ^{15}N: $Z = -1.068, P = 0.286$), the values of δ^{13}C and δ^{15}N of the holoparasite *C. songaricum* were closely correlated with those of its host, respectively (δ^{13}C: $r = 0.591, P = 0.004$; δ^{15}N: $r = 0.645, P = 0.001$) (Figures 3 and 4). When all the holoparasite samples were combined together, no significant enrichment or depletion of δ^{13}C and δ^{15}N was observed (δ^{13}C: $Z = -1.673, P = 0.094$; δ^{15}N: $Z = -1.178, P = 0.075$), but they were correlated with their corresponding hosts (δ^{13}C: $N = 22$, $P = 0.007$; δ^{15}N: $N = 22$, $P = 0.010$). We also found that the δ^{13}C versus δ^{15}N values were significantly correlated in the holoparasite *C. songaricum* but not for its hosts (holoparasite: $N = 44, P = 0.002$; host: $N = 44$, $P = 0.066$) (Figure 6(a) and (b)). Holoparasite/host variation in δ^{13}C was not correlated with variation in δ^{15}N ($N = 44$, $P = 0.863$).

4. Discussion

The analysis of the natural abundances of stable isotopes in plants is a powerful tool to explore water use efficiency [32,33]. The δ^{13}C values have been proven to be positively correlated with water use efficiency of plants. We found that the host plant *N. tangutorum* at the Tibetan plateau shows more negative δ^{13}C values than *N. sibirica* from the Gobi desert. However, these results do not agree with previous studies that δ^{13}C values of plants tend to increase with increasing elevation [28–30,34], reflecting a relatively free use of water and a lower water use efficiency of

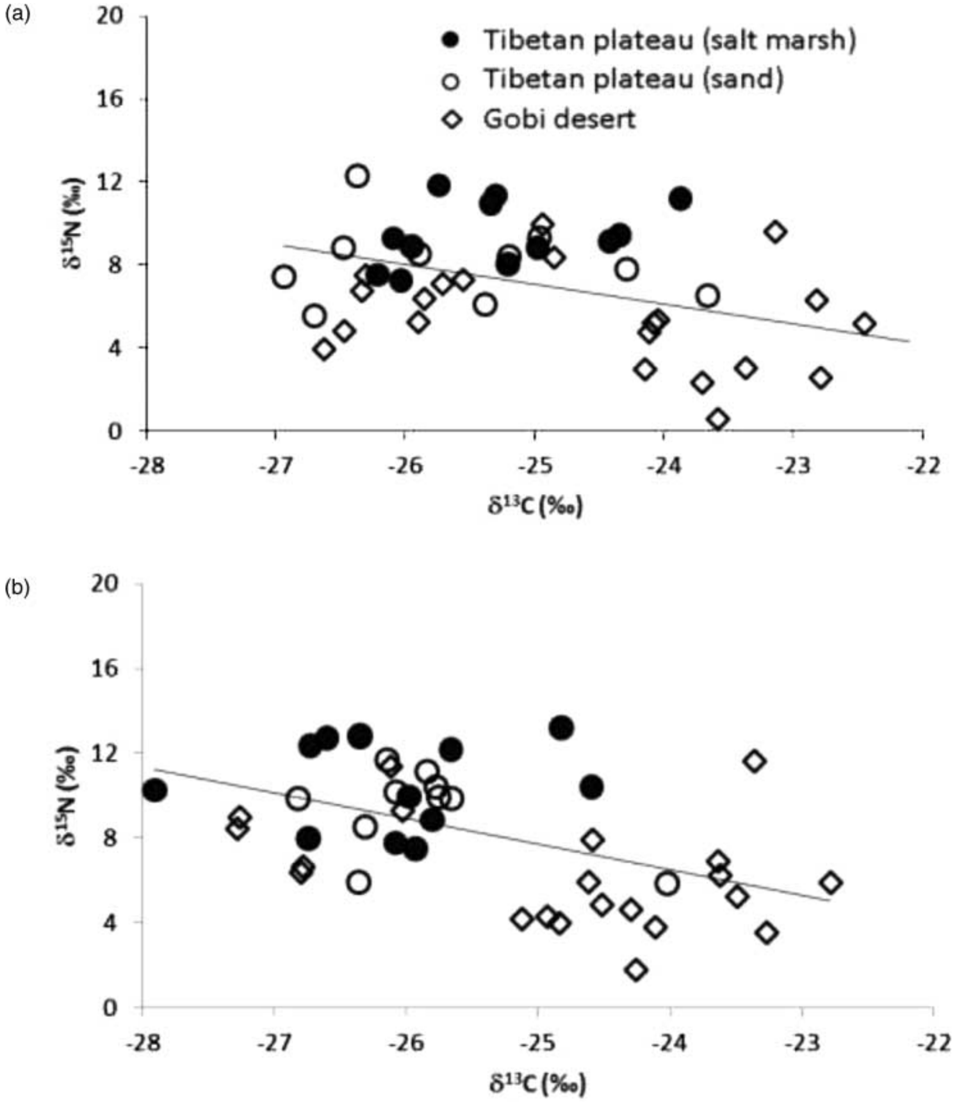

Figure 6. The δ^{13}C values of hosts and holoparasite *C. songaricum* from the Tibetan plateau and the surrounding Gobi desert plotted against their δ^{15}N values. (a) hosts; (b) holoparasites.

N. tangutorum at the Tibetan plateau. It has to be kept in mind that *C. songaricum* parasitises different host species at the Tibetan plateau and the surrounding Gobi deserts. There might be differential fractionation because of species differences independent of elevation. Although δ^{15}N values are higher in *N. tangutorum* than in *N. sibirica*, the relationships between δ^{13}C and δ^{15}N values of both the holoparasites and hosts are significantly and negatively correlated, mirroring the nutritional relationship between the holoparasites and hosts. Our study indicates that tissue samples with more negative δ^{13}C values tended to have more positive δ^{15}N values, as shown by Bolin *et al.* [5]. However, when differences between the holoparasite and host δ^{13}C values were plotted against the differences between the holoparasite and host δ^{15}N values, no significant correlation was observed, reflecting a segregation of δ^{13}C and δ^{15}N enrichment within the holoparasite tissues.

Table 2. Comparison of differences in δ^{13}C and δ^{15}N values between parasites and hosts in literature and our study.

Parasitic type	Difference in δ^{13}C values between parasite and host	Difference in δ^{15}N values between parasite and host	References
Root holoparasite	−0.5 ‰	1.25 ‰	This study
Root holoparasite	−0.97 ‰	2.40 ‰	[5]
Root holoparasite	1.5 ‰	–	[27]
Root holoparasite	No difference	–	[7]
Root holoparasite	3.5–6.0 ‰	–	[41]
Root holoparasite	No difference	Enriched	[39]
Root hemiparasite	−1.2 ‰	–	[27]
Mistletoe	−0.62 ‰	−0.71 ‰	[25]
Mistletoe	Depleted	No difference	[42]
Mistletoe	−1.90 ‰	–	[27]
Mistletoe	−0.24 ‰	–	[40]
Mistletoe	−1.98 ‰	−0.65 ‰	[21]

We observed consistent differences in δ^{13}C and δ^{15}N between *C. songaricum* and their host plants (*N. tangutorum* and *N. sibirica*) across the sampling sites at the Tibetan plateau and the surrounding Gobi desert, suggesting that the stable isotope signatures of holoparasites *C. songaricum* follow those of their hosts along different environment gradients (e.g. elevations and habitats). Nevertheless, we found that the holoparasite *C. songaricum* is significantly depleted in δ^{13}C but more enriched in δ^{15}N compared to its hosts. Our results are not consistent with previous studies that have found that a less negative holoparasite δ^{13}C value and a decreased δ^{15}N value are always observed relative to their hosts [6,21,25,27,35]. Despite an underlying assumption that complete heterotrophy will result in identical parasite/host δ^{13}C signatures, we found significant differences in δ^{13}C values between the holoparasite *C. songaricum* and its host *N. tangutorum* roots at the Tibetan plateau at high elevations (Figure 3), which supports the previous observations that δ^{13}C values of parasites are depleted compared to hosts regardless of parasitic types (holoparasite, hemiparasite or mistletoe) [5,21,25,27,36,37]. This inconsistency can be attributed to δ^{13}C partitioning within the tissue types and organs of hosts [5,24,38] (Table 2). Badeck *et al.* [39] report that, on average, roots are 1.91 ‰ enriched relative to leaves, which can explain the holoparasite/host δ^{13}C values in our study. Our results show that not all holoparasitic plants are characterised by less negative δ^{13}C values compared to their hosts [7,40], in agreement with the results of Kraus *et al.* [41].

Our results support previous studies that show that host and holoparasite δ^{15}N values are significantly correlated [5,36] (Table 2). However, δ^{15}N values of the holoparasites and hosts in our study show an average holoparasite/host difference of +1.34 ‰ and +1.15 ‰ for *N. tangutorum* and *N. sibirica*, thus failing to support the underlying assumption of virtually identical δ^{15}N signatures for the holoparasites and hosts [36]. Although variation in the N isotope values of our samples could result from the deep root systems [42], it seems more likely that variation in the ^{15}N isotopic composition of the holoparasites and hosts is a result of contrasting strategies of resource acquisition of nitrogen of *C. songaricum*. We notice that there are a great number of adventitious roots that originate from deeply-buried fleshy stems of *C. songaricum* (Figure 1(b)). The presence of adventitious roots implies that *C. songaricum* in northwest China is likely to be a carbon root parasite but the enriched δ^{15}N values suggest that it would rely on other resources for nitrogen acquisition [5,40]. Along with previous studies [5,24,38], our results suggest that the isotope enrichment of parasites compared to hosts may vary when different organs or tissues of hosts are considered. In addition, the adventitious roots were often found at the upper part of the stem of *C. songaricum*. Future studies should aim to test the effects of host tissue specificity and sampling depth to investigate the isotopic difference between the holoparasites and hosts. A study of this kind would help to improve the understanding of nutritional relationships between

C. songaricum and its hosts typically distributed at the Tibetan plateau and the Gobi desert in northwest China.

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