Cost-benefit Quantification of Leaf Carbon Economics to Disentangle Responses of Plant Assemblages to Deer Herbivory

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Research Article

Keywords: Cost-benefit, Plant strategy, Physiological traits, Herbivory, Community

Posted Date: June 7th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-539198/v1

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Cost-benefit quantification of leaf carbon economics to disentangle responses of plant assemblages to deer herbivory

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Author Contributions: YW and KN conceived, designed, and performed the experiments. All authors analyzed the data. YW wrote the manuscript; other authors provided editorial advice.
Abstract

Although the plant carbon cost-benefit balance is known to be related to individual plant growth, reproduction, and population expansion, the association with plant community differences is not well understood. In this study, we examined how the leaf carbon cost-benefit metrics were associated with the assembly process of forest understory plant communities in areas highly affected by deer browsing. We calculated these metrics from plant physiologically parameters for 14 forest floor plant species growing in deer presence/absence site to detect the relationship between species dominance and leaf carbon cost-benefit metrics. As a result, the patterns of interspecific variation in benefit along the plant dominance rank differed in deer presence/absence sites, contributing to the marked differences in species composition and diversity observed at the two sites. In the absence of deer, where competition was the dominant determinant of plant community composition, carbon benefits among species were positively related to the plant dominance rank, indicating that species able to acquire more carbon were at an advantage. On the other hand, under deer herbivory, differences in carbon benefit between species were not strongly apparent and were not related to the plant dominance rank, indicating few differences in reproductive and expansion ability (plant fitness) between species. This process contributes to the high species diversity of plant communities observed in the presence of deer. Our results emphasize the possibility of connecting different fields of studies, physiological ecology, community ecology, and the plant carbon cost-benefit balance of single leaves to explain plant community composition differences.

Keywords: Cost-benefit, Plant strategy, Physiological traits, Herbivory, Community
Introduction

One of the major goals of plant community ecology is to gain a mechanistic understanding of how a wide variety of factors contribute to the determination of community diversity, richness, and composition in a spatiotemporally heterogeneous environment (Cadotte et al., 2009; Pavoine & Bonsall, 2011; Spasojevic & Suding, 2012; HilleRisLambers et al., 2012).

Assessing the determinants of community composition can also help us understand the response of ecosystems to human-induced environmental changes and disturbances, which can lead to the development of appropriate management approaches (Webb et al., 2010; Mori, 2011; Mori et al., 2013, 2015; Bjorkman et al., 2018). Currently, the trait-based approach is becoming increasingly important in understanding plant communities’ responses to environmental conditions (Cadotte et al. 2013; Mori et al. 2013). Each plant trait, which is realized through many ecological and evolutionary processes, fundamentally reflects the strategies of plant growth, survival, and reproduction (Kattge et al., 2020).

Individual plants respond to their growing environments by altering their forms to maximize plant carbon benefit, which is the amount of carbon acquired via photosynthesis subtracted from the costs of producing and maintaining the individual plants. Plant carbon benefit determines the growth and reproduction of individuals and ultimately drives population expansion (Field, 1983; Kudo, 1992; Kikuzawa, 1995a; Ackerly, 1999).

Importantly, plant carbon benefits are often quantified on the basis of individual leaves. Researchers have been trying to build the “cost-benefit model” of leaf photosynthetic carbon production to estimate the optimal plant strategies for leaf longevity in growing environments (Chabot & Hicks, 1982; Kikuzawa & Kudo, 1995; Eamus et al., 2000). Because of the high degree of autonomy of individual plant organs, realizing a positive carbon balance at the level
of individual leaves fundamentally contributes to optimal whole-plant performance (Sprugel et al. 1991). However, much uncertainty still exists regarding how carbon assimilation and the resultant cost through intrinsic (e.g., respiration) and extrinsic (e.g., herbivory) can be summed up to the community-wide consequences through the responses of individual plants and each of the constituent species. To fill this knowledge gap, functional trait ecology needs to further acknowledge the dynamic features of plant traits. For example, the photosynthetic ability of individual leaves changes over time to achieve positive outcomes of net carbon balance. Combining this information with well-measured plant traits is the first step.

Plant strategies generally vary according to one principal axis of the trade-off between resource acquisition and conservation (fast and slow), which is inferred from plant characteristics, especially leaf traits (Wright et al., 2004; Reich, 2014; Onoda et al., 2017). The acquisitive plant strategy is characterized by low investment in leaf structure and high photosynthetic efficiency. This strategy is advantageous when the risk of losing leaves is relatively high (a short leaf lifespan), especially under disturbance pressure, because it allows for the offset of carbon investment in leaf structure in a short time considering the carbon cost-benefit methods. This strategy is often considered the fast end of a plant economic spectrum. In contrast, the slow end of the spectrum is characterized by a conservative strategy with high investment in leaf construction and maintenance, requiring a long leaf lifespan. These features, based on a longer time horizon, enable plants to acquire more carbon per leaf, which is advantageous in competition for light under stable environmental conditions. This fast-slow axis in strategies is observed both inter- and intraspecifically (Wakatsuki et al. 2021), importantly guiding the discipline to gain a comprehensive understanding of how the structure and composition of plant species assemblages respond to the fluctuating environment (Kraft et al., 2008, 2015).
Forest floor plant communities are known to account for much of the diversity in forests due to their spatial and temporal environmental heterogeneity (Gilliam, 2007). In recent years, there has been an increasing recognition that anthropogenic influences can substantially alter these ecological communities due to land conversion, biological invasion, and an overabundance of herbivores (Whigham, 2004; Gilliam, 2006; Landuyt et al. 2019). In particular, the increasing overpopulation of ungulates is causing major problems worldwide (Côté et al., 2004). They are known to affect ecosystems directly and indirectly through browsing, trampling, and altering carbon and nutrient cycling (Hobbs, 1996; Augustine & McNaughton, 1998; Rooney & Waller, 2003; Kasahara et al., 2016). Here, we focused on the physiological response of forest floor plants to deer herbivory, represented by the amount of carbon acquired by leaves, in order to examine the mechanisms that determine community composition under deer herbivory. We infer differences in the mechanisms of determining plant species composition between deer presence and absence by observing the carbon cost-benefit balance related to species-specific strategies.

First, we estimated the annual leaf carbon benefit of multiple forest floor plant species and quantified how the benefits related to plant species dominance in the presence and absence of deer. We assumed that species with larger leaf carbon benefits would have an advantage over other species by allowing them to invest more carbon in species expansion and reproduction. Second, we examined how deer herbivory alters the leaf carbon balance of species and how this affects the determination of the species composition of the community under deer herbivory. We hypothesized that the optimal strategies represented by the carbon cost-benefit balance would be different in the presence and absence of deer, resulting in different species composition. To address the above issues, we selected deer exclosure fences established in a cool temperate forest in northern Japan, where deer overabundance is
currently an issue, as our study area (Nishizawa et al. 2016; Fujii et al. 2017; Wakatsuki et al. 2021). We compared plant community composition between deer presence and absence sites. Our goal was to expand our understanding of the establishment process of plant communities from the physiological indicators directly related to plant dominance based on plant carbon cost-benefit balance during the growing season instead of the traditional indirect approach using snapshot functional traits.

Methods

Study Site

The study was conducted in the Horobetsu area of Shiretoko National Park (44°06’00”N 145°01’42”E) in Hokkaido, Japan. This park was registered as a World Natural Heritage Site by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) because of its high biodiversity due to the relationship between the marine and terrestrial ecosystems (https://whc.unesco.org/en/list/1193). The mean annual temperature is approximately 6.69 °C, and the mean annual precipitation is approximately 1322 mm (at Utoro Sharigun, between 2011 and 2020, http://www.data.jma.go.jp/obd/stats/etrn/index.php). The forest here is a boreal forest characterized by a mixed coniferous and broad-leaved natural forest dominated by *Abies sachalinensis*, *Quercus crispula*, and *Kalopanax septemlobus* (The Forestry Agency of Japan 2004). The forest floor is usually covered with snow from the end of November to early May (https://www.jma-net.go.jp/sapporo/index.html).

In this area, deer (*Cervus nippon yesoensis*) over-abundance has been a problem since the late 1980s, and the herbivores have dramatically changed the vascular plant community (Tokida et al., 2004). Our study site, Horobetsu, has one of the highest deer
densities in the area. Since 2010, the density has been as high as approximately 10 deer/km, as estimated by light censuses conducted in spring (http://dc.shiretoko-whc.com). To recover the ground-layer plant community, a “deer exclosure fence” was built in this area in 2003, and since then, there has been a noticeable increase in understory plants inside the fence.

**Field data collection**

The exclosure plot was protected from deer herbivory by the fences, and the control plot was exposed to herbivory. The size of the exclosure and control plots were 80 m × 120 m (0.96 ha) and 100 m × 100 m (1.00 ha), respectively. These plots were located close to each other so there was little difference in the woody plant community composition (The Forestry Agency of Japan 2004). Both plots were originally similar forest floor plant communities and were under equivalent browsing pressure by deer before the exclosure fence was built. In these plots, quadrats (1 m × 1 m) were placed at 10m intervals; there were 95 exclosure quadrats and 100 control quadrats. One quadrat was not included because of a fallen tree in the exclosure plot. These quadrats were established in 2014 (Nishizawa et al., 2016). In each quadrat, forest floor plant species were identified, and percent cover of each species was visually estimated in units of 1%. Here, we defined “forest floor plants” as herbaceous plants, ferns, and vines, and excluded the seedlings of semi-tall tree species. In the case of species coverage less than 1%, we recorded the appearance. We conducted this study during the plant growth period (from the end of June 2020).

**Calculation of expected leaf carbon benefit and cost metrics**
We used 14 forest floor species that appeared in both plots in the field study (supplementary material: S1) to evaluate the difference in leaf carbon gain and cost metrics in the deer presence and absence sites. We collected five leaf samples for each species for each treatment (control and exclosure), during the plant growth period (as of the end of August in 2018 and 2019). We selected only the fully formed leaves. We estimated the total leaf carbon gain ($TCG: g$), total leaf carbon cost ($cost: g$), and leaf carbon benefit ($benefit: g$) of the collected leaves. These are expected values that take into account leaf life span and leaf growth during the plant growing season in the calculation. These three metrics were calculated from six parameters: expected leaf longevity ($LL: \%$), leaf area ($LA: m^2$) change with growth, daily light intensity ($PAR$), daily leaf carbon gain ($DCG: g$), leaf producing carbon cost ($LPC: g$), and daily leaf maintaining carbon cost ($LMC: g$). We set the plant growing season as the period from May to November (210 days) when the ground was usually not covered with snow.

**Parameter 1. Expected leaf longevity**

The probability of leaf persistence during the growing season was used as the leaf longevity ($LL: \%$) (Supplementary materials: S2). We marked the leaves in May 2019. After that, we checked the counts of the remaining leaves three times (at the end of June, August, and October in 2019). We calculated the probability of leaf persistence per day ($\%$) for each species and treatment (control and exclosure). We confirmed that the leaf mortality rate and browsing opportunity by deer did not change depending on whether they were marked. We assumed that all species would be defoliated by the end of the plant growing season (the end of November).
Parameter 2. Leaf area change with growth

We measured the leaf area of collected samples from scanned images using ImageJ software (Rasband 1997–2014), and this size collected in August was assumed to be the fully grown leaf size. To account for the increase in leaf size in calculating leaf carbon gain and cost metrics, we estimated the change in leaf area of collected samples by the mean values of the size expansion rate of marked leaves for each species and each treatment (used in the estimation of leaf longevity [LL]). We measured the length and width of marked leaves for each species and each treatment three times during the growing season (the end of May, June, and August). To estimate the leaf area from the leaf length and width, equations between leaf area and the values multiplied by the leaf length and width were obtained for each species in advance using our scanned image data (Supplementary material: S3). We calculated the leaf area (LA: m²) for each day during the growing season from the mean values of the size expansion rate during each measurement period (from the end of May to the end of June and from the end of June to the end of August). For all species, it was assumed that leaf area started at zero and that there would be no change in leaf area after September.

Parameter 3. Light intensity (photosynthetically active radiation)

Photosynthetically active radiation (PAR) was measured using a sensor (Quantum Sensor MIJ-14PAR Type2/K2, Environmental Measurement Japan) for one year from September 2019, and data for May-November (plant growing season) were used for the analysis (Supplementary materials: S4). Sensors were placed on the ground in both plots (control and exclosure) at the same level as the height of the understory plants. The PAR was recorded...
once every 10 min \((i; 144 \text{ times per day})\) and used as \(PAR\) for a 10-minute period. The average \(PAR\) of the two locations was used as the annual value, and the average of each of the five days was used for the analysis to improve normality.

**Parameter 4. Daily leaf carbon gain**

Daily leaf carbon gain \((DCG)\) was calculated from the net \(\text{CO}_2\) assimilation rate \((A; \mu\text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1})\), which was inferred from the photosynthetically active radiation \((PAR\) response curve of linear electron flow \((LEF)\) (Supplementary material: S5), and leaf longevity \((LL)\).

We measured \(LEF\) using Multispec v.2.0, (Kuhlgert et al., 2016) in study plots from the end of June until early July in 2019. Multispec can measure the photosynthetic efficiency index at the current light intensity in a short time without damaging the leaves. To obtain the \(PAR\) response curve of \(LEF\) for each species, we measured the \(LEF\) at various light intensities for each species (Supplementary material: S5). The curve equations were derived using a nonlinear regression.

\[
LEF = a \times \log\left(\frac{PAR}{a} + \exp\left(-\frac{b}{a}\right)\right) + b \quad \cdots (1.1)
\]

where \(a\) and \(b\) are species-specific values. From equation 1.1, we estimated the \(PAR\) response curve of \(A\), referring to Flexas et al. (2002):

\[
A = c \times LEF \quad \cdots (1.2)
\]

where \(c \approx 0.103\) is the coefficient for calculating \(A\) from \(LEF\), calculated based on Flexas et al. (2002), which shows the relationship between \(\text{ETR}(\approx LEF)\) and \(A\). We calculated the \(DCG\) of each leaf sample using equation 1.2, \(PAR\) data recorded once every 10 min (144 times per
day, details in parameter 4), the change in leaf area with growth \((LA: \text{m}^2, \text{details in parameter } 2)\), and leaf longevity \((LL: \%, \text{details in parameter } 1)\):

\[
DCG_t = \sum_{i=1}^{144} A_i \times LA_t \times LL_t \times d       \quad \cdots (1.3)
\]

where \(d\) is the value used to convert the unit of measure from \(\mu\text{mol CO}_2 \text{s}^{-1}\) to grams. The \(DCG\) estimates daily carbon gain (g) on day \(t\) using \(PAR\) at every 10 minutes interval \((i)\).

Parameter 5. Leaf-producing carbon cost

Leaf carbon content was used as the leaf-producing carbon cost \((C: \text{g})\) (Supplementary materials: S6). We calculated it by multiplying leaf dry mass by the ratio of carbon in collected leaves measured by an NC analyzer (Sumigraph NCH–22 F, Sumika Chemical Analysis Service, Japan).

Parameter 6. Daily leaf maintaining carbon cost

Daily leaf maintaining carbon cost \((LMC: \text{g})\) is defined as the amount of carbon consumed per day through respiration. It was calculated from dark leaf respiration rate \((R: \text{nmol g}^{-1} \text{s}^{-1})\), which was inferred from leaf nitrogen concentration \((N: \text{mmol g}^{-1})\) referring to Reich et al. (2008):

\[
\log R = 1.078 \times \log(N) + 0.911
\]

\[
R = 10^{1.078 \times \log(N) + 0.911} \quad \cdots (2.1)
\]

We calculated \(N\) by using the ratio of nitrogen in the dry mass of collected leaves measured by an NC analyzer (Sumigraph NCH–22 F, Sumika Chemical Analysis Service, Japan). Leaf
mass per area \((LMA; \text{g m}^{-2})\) was calculated by dividing the leaf area of collected samples by
the respective leaf dry masses to estimate the change in leaf dry mass \((DM; \text{g})\) with the
change in leaf area with growth \((LA; \text{m}^2\text{, details in parameter 2})\):.

\[
DM_t = LA_t \times LMA \quad \cdots (2.2)
\]

\(DM\) estimates leaf dry mass on day \(t\). We assumed that \(N\) and \(LMA\) measured in the collected
leaf samples did not change during the growing periods. We calculated the \(LMC\) of each leaf
sample using equations 2.1 and 2.2:

\[
LMC_t = R \times DM_t \times LL_t \times e \quad \cdots (2.3)
\]

where \(e\) is the value used to convert the unit of measure from nmol s\(^{-1}\) to gram. The \(LMC\)
estimates the carbon cost (g) by leaf respiration on day \(t\).

We calculated total leaf carbon gain \((TCG; \text{g})\), total leaf carbon cost \((cost; \text{g})\), and leaf carbon
benefit \((benefit; \text{g})\) of collected leaf samples using the above six parameters, referring to
Kikuzawa (1995b). \(TCG\) is the sum of the daily leaf carbon gain \((DCG)\) for the plant-growing
season.:  

\[
TCG = \sum_{t}^{1-210} DCG_t
\]

\(TCG\) estimates the total carbon gain during the growing season by the sum of carbon gains on
day \(t\) (210 days: during growth periods).

\(Cost\) is the sum of the daily leaf-maintaining carbon cost \((LMC)\) during the growing season
and the leaf producing carbon cost \((LPC)\):  

\[
Cost = \sum_{t}^{1-210} LMC_t + LPC
\]
Cost estimates the expected total carbon cost of producing and maintaining leaves during the growing season by the sum of carbon cost on day t and leaf-producing carbon cost.

Benefit was the net profit of the leaf obtained during the growing season by subtracting the cost from TCG:

\[ Benefit = TCG - Cost \]

Data analysis

We first compared plant community composition between the control and exclosure plots to clarify their differences in the presence and absence of deer. Species richness (number of species in quadrats) was used as a measure of diversity. We constructed a rank abundance curve, which is a chart depicting both species richness and species evenness, to evaluate the differences between the two communities.

Next, we confirmed the correlation between total carbon gain and benefit along species dominance rank for each plot to examine how leaf carbon gain was related to plant dominance. The species dominance rank for each plot was determined based on the abundance of species in each plot. We assumed carbon cost as an indicator of species’ carbon resource investment strategies and confirmed the correlation in carbon cost among species along the species dominance rank. The larger and smaller carbon cost implies that more and less carbon is invested in the production and maintenance of leaves, respectively (more conservative and acquisitive strategy, respectively).
Results

Plant community composition

In the two plots (including 100 quadrats in the control plot and 95 quadrats in the exclosure plot), we recorded 51 species. There were 41 plant species in the control plot and 39 plant species in the exclosure plot. Species richness was higher in the control plot than in the exclosure plot (Supplementary material: S7). The mean (± SE) species richness was 7.03 (± 0.29) and 5.05 (± 0.19) in control and exclosure, respectively. *Toxicodendron orientale* was the most frequently observed species in both plot types. Exclosure plots were characterized by many individuals of *Maianthemum dilatatum* and *Sasa kurilensis*. Conversely, control plots were characterized by the abundance of *Hydrangea petiolaris* and *Sasa spiculosa* in the understory stratum. The predominance of several unpalatable species, often observed under deer browsing pressure, was not seen in the control plots. The rank-abundance curve showed a steeper gradient in the exclosure than in the control (Supplementary material: S8). This means a large difference in dominance between dominant species (high-ranking species) and rare species (low-ranking species) in the exclosure plots. The order of abundance of the 14 targeted species in each plot (Supplementary materials: S1) showed that the frequency of each species differed between the inside and outside of the fences. The targeted species in our study accounted for 61.7 percent and 71.6 percent of the total coverage in the control plots and the exclosure plots, respectively. *Sasa sp.*, one of the dominant species in both plots, was excluded from the target species because it is not deciduous in one year, making it difficult to estimate its carbon gain during the growing season.

Leaf carbon gain
Comparing each parameter that we used to calculate the metrics of leaf carbon benefit and cost between inside and outside the fence for each species, the leaf life span was longer, and the leaf carbon concentration was higher in deer absence plots than in deer presence plots (Supplementary materials: S2 and S6).

Figure 1 shows that species with higher total carbon gain and carbon benefit were more dominant in the exclosure plots. On the other hand, in control plots, total leaf carbon gain was higher for less dominant species than inside the fences, and there was no significant relationship between leaf carbon benefit and the dominance rank. Figure 2 shows that species with higher carbon costs in the leaves were more dominant in the exclosure plot. On the other hand, the opposite trend was observed in the control plot. The total carbon gain, leaf carbon benefit, and cost were greater in the exclosure plot than in the control plot, and the plasticity of these metrics was also greater in the exclosure plot (Supplementary material: S9).

Discussion

Plant community composition

Species composition and diversity differed between the inside and outside of the exclosure fences (supplementary materials: S1, S7 and S8). In the deer-excluded environment, plant diversity was lower than that in the deer-browsed sites. Previous studies here (Nishizawa et al. 2016; Wakatsuki et al. 2021) have suggested that the release of plants from deer herbivore pressure (by establishing the fences) leads to an environment with high plant coverage, where competition for light can be significantly intensified, leading to a low-diversity community dominated by a limited set of species that are superior in their ability to acquire light. In contrast, although plants are prone to herbivory disturbance, the presence of deer rela...
competition for light among species, enabling the coexistence of multiple species. In summary, the determinants of assembly processes change due to the presence or absence of herbivores, which shape local plant communities.

These trends, which were seen when comparing sites with and without deer, have been reported in other studies, and not only in this study area (Webster et al., 2017; Li et al., 2018; Sabo et al., 2019). We could infer that moderate browsing pressure contributes to the maintenance and enhancement of the diversity of the forest plant community (Stokely & Betts, 2020). Therefore, excluding deer with the aim of restoring plant diversity would not necessarily be effective and would move the system to an alternative, undisturbed ‘natural’ state resulting from the termination of herbivore browsing.

**Plant assembly mechanisms**

In the exclosure plots, species with a more significant total carbon gain and benefit had a higher dominance rank (Figure 1). Previous studies addressing invasive plants suggested that a greater leaf carbon gain allows for more investment in reproduction and expansion for species, leading to enhanced species dominance (Osunkoya et al., 2010; Shen et al., 2011). The existence of these species, which have advantages relative to others, is likely to result in low diversity environments dominated by certain species. Dominant species inside the fences had high carbon content (Figure 2); that is, they had a more conservative strategy. In addition, the leaf life span and leaf carbon concentration were greater in plants within the fences (Supplementary materials: S2 and S6). The absence of deer browsing pressure may allow for a longer leaf lifespan, resulting in a more carbon-invested leaf (Wright et al., 2004). These results suggest that species investing more in their leaf structures dominate environments.
without ungulate browsing. Features of carbon-invested leaves, such as large leaf size and strong leaf structure, are advantageous in competition for resources (Smith, 1982; Bartemucci et al., 2006; Kunstler et al., 2016). At excluded deer browsing sites, species with a conservative strategy (investing carbon in leaf structure) have an advantage over other species in competition for resources, resulting in greater carbon acquisition for these species. We assume that this process leads to the establishment of an environment suitable for certain competitive species that is relatively low in diversity.

In contrast, in the control plots, total carbon gain was higher in lower dominance rank species, and there were no differences in benefit among species along the dominance rank (Figure 1). This finding indicates that the amount of total carbon gain does not lead to species dominance; in contrast to the exclosure plot, the species with larger total carbon gains are less dominant. In addition, interspecific differences in benefits are smaller in the control than in the exclosure (Supplementary material: S9). It seems that deer herbivory pressure reduces the interspecific difference in carbon benefit, and as a result, the difference in reproductive and expansion ability (plant fitness) among species is also reduced. This equalizing mechanism that reduces interspecific differences in fitness might be a factor enabling multispecies coexistence under deer herbivory (Chesson, 2000; Leibold and McPeek 2006). The dominant species in the control plot had leaves with low carbon costs (Figure 2), suggesting that these species have a fast strategy. Previous studies have suggested that species with less costly leaves, i.e., small leaf size and low leaf toughness, are advantageous under browsing pressure (Webster et al., 2017; Boulanger et al., 2018). These features allow plants to achieve a positive carbon balance in leaves within a short time (Kikuzawa, 1995b; Navas et al., 2003). Moreover, given that deer browsing pressure can substantially shorten leaf lifespan—the potential of investment failure (Supplementary materials: S2), the strategy to
quickly reach out to the positive leaf carbon balance as much as possible within a limited time
is likely to be advantageous under deer herbivory (Chabot & Hicks, 1982; Matsuki & Koike,
2006). It is considered that herbivory reduces the difference in survival advantage among
species, resulting in the establishment of a highly diverse environment. This effect could also
be the fundamental mechanism underlying the intermediate disturbance hypothesis, in which
intermediate disturbance contributes to the maintenance of diversity (Connell, 1978; Hobbs &
Huenneke, 1992; Olff & Ritchie, 1998).

In conclusion, our results suggest the significance of observing the carbon balance of plants in
clarifying the community assembly process. Differences in carbon cost-benefit metrics among
species could be a more direct indicator of survival strategies than others, reflecting
differences in plant morphological, physiological, and phenological features, such as leaf size,
photosynthetic efficiency, and leaf longevity. Furthermore, this metrics can provide a measure
that reflects differences in the fitness of individuals and species, which is crucial for
understanding community assembly (Saito et al. 2021). Plant carbon cost-benefit analysis is a
topic that has long been studied as an indicator of survival strategies, but the present study
demonstrates its novel importance in understanding plant community composition. The
evaluation of community composition based on individual leaves in this study might be an
overestimation because we could not confirm the carbon balance of the whole plant, including
aboveground and belowground parts. Nevertheless, we believe that our approach, which
focuses on cost-benefit analysis based on individual leaf level, provides a more realistic
explanation of species dominance than the trait-based approach and is useful for a more
delineated understanding of plant community assembly processes. The study results
emphasize that connecting research from different fields, physiological and community ecology, can lead to fresh ecological insights.

**Acknowledgements**

We thank S. Masumoto, K. Okada, Y. Kobayashi, T. Takatori, K. Suzuki and S. Horiuchi for their contribution to our study. Logistical support for the field study provided by the Shiretoko Nature Foundation.

**Declarations**

**Funding**

This study was supported by the Mitsui & Co., Ltd. Environment Fund (R17-0062) and Grant-in-Aid for JSPS Fellows (17J11540).

**Conflicts of interest/Competing interests**

Authors declare that they have no conflict of interest.

**Ethics approval**

Not applicable

**Consent to participate**

Not applicable

**Consent for publication**

Not applicable

**Availability of data and material**

These are available from the corresponding author upon reasonable request.
Code availability

These are available from the corresponding author upon reasonable request.

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Figures

Figure 1

Correlation between total carbon gain (gray line) and benefit (colored line) and plant species abundance rank. Orange and green points show the data measured in the control plot and in exclosure plot, respectively. Significant are evaluated by Kendall rank correlation coefficient (n.s: $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

Figure 2

Correlation between carbon cost and plant species abundance rank. Orange and green points show the data measured in the control plot and in exclosure plot, respectively. Significant are evaluated by Kendall rank correlation coefficient (n.s: $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
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