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学位論文題名

Physiological basis for carbon isotope dendroclimatology in Siberia

（シベリアで炭素同位体を用いた年輪気候学的研究を行うための生理学的基礎）

学位論文内容の要旨

The larger temperature increase is expected in continental regions at high latitude. The climate change will alter growth pattern of boreal tree species, causing change in the size of their carbon reservoir. Dendroclimatological analysis is an effective tool to elucidate growth response of the tree species to expected climate change with a long-term perspective, which is enabled by the use of tree rings. Extension of climate proxy data is therefore necessary for elucidating growth response of boreal trees to the climate change. By developing not only tree rings width and density but also stable isotope chronology, we can extract as much information from tree rings as possible. The development of multi-proxy chronology of tree-ring width, density and isotope ratios also helps for climate reconstruction in Siberia, where spatial resolution of climate proxy records is relatively lower. However, isotope dendroclimatology is still in its infancy and basic physiological processes as to how environmental information contained in $\delta^{13}C$ of photosynthetic carbon is eventually reflected as fluctuations of tree-ring $\delta^{13}C$ remains unexplored. Post-photosynthetic processes such as translocation, storage and remobilization of photoassimilate are closely related to intra-annual isotopic variation of tree rings.

Firstly, in order to study translocation process, pulse-labeling of branches of straight-grained *Cryptomeria japonica* D.Don and helical-grained *Larix gmelinii* (Rupr.) Rupr. growing in a temperate and a continuous permafrost zone, respectively, was conducted with stable $^{13}CO_2$. ^{13}C spiral translocation paths closely related to the respective spiral and helical grain (the arrangement of phloem sieve cells with respect to the tree axis) were observed. ^{13}C tracer pulse-labeled in May and September reached tangentially different locations, suggesting seasonal change in the pathway of carbohydrates.

Secondly, in order to clarify the seasonal course of carbon allocation and storage patterns among needles, branches, stem and roots, I pulse-labeled ten *Larix gmelinii* (Rupr.) Rupr. June photoassimilate was mainly allocated to aboveground parts, suggesting active aboveground growth in spring. Very little was allocated to belowground parts (2.6-7.9 %), potentially because of root growth inhibition at the low soil temperature in spring. On the other hand, a higher proportion of July and August photoassimilate was allocated to belowground parts (32-44 % and 12-24 %, respectively). The starch pool in non-needle parts, which can be

used for xylem formation, drew about 43 % of its carbon from previous year's photoassimilate. Analysis of intra-annual $\delta^{13}C$ of the tree rings formed after the labeling revealed that earlywood contained photoassimilate from the previous summer and autumn as well as from the current spring. Latewood was mainly composed of photoassimilate from the current year's summer/autumn, although it also relied on stored material in some cases. The results suggest the need for separating earlywood and latewood for paleoclimate reconstructions.

Thirdly, in order to examine whether or not drought in eastern Siberia limits radial growth, I studied the relationships between early-/latewood width, stable carbon isotope ratio ($\delta^{13}C$) of holocellulose, and soil moisture at a dry and a wet site, which differed considerably in soil water conditions. Recharge of soil water by snowmelt in spring and subsequent drought in summer provided a marked seasonal contrast in soil water conditions between the early- and latewood formation period. Ring index was calculated by dividing each early-/latewood width by the 5-yr averaged width for each individual. In order to determine whether drought influenced the ring index – $\delta^{13}C$ relation, the ring index time series were compared with $\delta^{13}C$ time series. I collected wood samples from eight *L. gmelinii* and four *Pinus sylvestris* L. trees from the two sites and measured the early- and latewood widths and $\delta^{13}C$ of early- and latewood formed during the years 1996-2000. At the dry site, seasonal soil water content variation corresponded to seasonal $\delta^{13}C$ variation of tree rings. I found negative ring index – $\delta^{13}C$ correlations in latewood for both species at the dry site mainly dominated by *P. sylvestris*, but not in latewood of *L. gmelinii* at the wet site dominated by *L. gmelinii*. Decrease and/or early cessation of latewood growth and increase in $\delta^{13}C$ under drought conditions possibly explain this negative correlation. This suggests the growth limitation of trees in this region by drought and the prospects of reconstructing past drought with latewood $\delta^{13}C$ of the dry site.

Lastly, I established a long-term $\delta^{13}C$ record of *P. sylvestris* tree rings from the dry site for the recent 100 years. As predicted from the preliminary studies, the latewood $\delta^{13}C$ showed a significant negative correlation to July precipitation ($r = -0.33$, $P < 0.01$) and a positive correlation to July temperature ($r = 0.35$, $P < 0.01$), while weaker but significant correlations to June and July temperature and June precipitation were found with the earlywood $\delta^{13}C$. Observed dampening of climate signal in earlywood is attributed to the use of carried-over photoassimilate for earlywood formation. In fact, earlywood $\delta^{13}C$ was significantly correlated to the latewood $\delta^{13}C$ of the previous year ($r = 0.42$, $P < 0.01$), suggesting the carry-over of photoassimilate.

Our results proved that post-photosynthetic processes such as translocation, storage, and remobilization of storage are related to anatomical structure and physiological function of trees and the post-photosynthetic processes can significantly alter isotope signals of photosynthate, suggesting the need to understand the biological processes for improved quality of climate reconstruction with tree rings. Most isotope dendroclimatological studies have utilized whole tree rings for climate reconstruction, assuming carry-over of storage carbon is negligible. However, our results suggested the need to separate earlywood and latewood, especially when working on long-living trees with narrow tree rings, where slow carbon metabolism is expected.

学位論文審査の要旨

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（シベリアで炭素同位体を用いた年輪気候学的研究を行うための生理学的基礎）

本論文は東シベリアに優占するダフリアカラマツ（*Larix gmelinii* (Rupr.) Rupr.）及びヨーロッパアカマツ(*Pinus sylvestris* L.)の年輪の安定炭素同位体比を用いた気候復元及び気候応答解析を行うため必要な樹木生理学的な基礎的情報を明らかにしたものである。葉での光合成生産と年輪形成をつなぐ転流・貯蔵プロセスを $^{13}CO_2$ ラベリングにより追跡した結果、転流した光合成産物は円周方向に拡散せず樹冠の一方向に配分されること、光合成産物はその年の年輪形成だけではなく、翌年まで貯蔵・繰り越されて年輪形成につかわれることが解明された。また、配分および貯蔵は季節的に変化し、春の光合成産物は活発な展葉・シュート伸長・肥大成長のため、ほとんどが地上部に配分され（93-97%）、地下部には 2.6-7.9%しか配分されなかったが、夏（７月）と秋（８月）の光合成産物は地下部にそれぞれ 32-44%、12-24%配分され高い地下部への配分が見られた。早材の形成は当年の春と前年の夏・秋から繰り越された貯蔵物質の両方を利用していたが、晩材はほぼ当年の光合成産物のみを利用しており、土壌水分に大きな季節変化が見られる東シベリアにおいて気候復元を行う際には、早材と晩材を分けて同位体比を測定するなど、季節性を充分に考慮する必要性が示唆された。

東シベリアヤクーツクにおいて、気象および水文学的なデータが揃っている最近の５年分の年輪について、年輪の幅・密度、炭素同位体比を測定し、水分環境との相関を解析した。晩材の炭素同位体比は成長期間降水量と $\delta^{13}C$ の間に有意な負の相関が見られ、最も乾燥した条件で形成される乾燥サイトの晩材では幅と $\delta^{13}C$ の間に有意な負の相関が、最も湿潤な条件で形成される湿潤サイトの早材では弱い正の相関が見られ、晩材形成過程は乾燥によって制限されうることが示された。以上の結果は、晩材 $\delta^{13}C$ が過去の土壌水分環境を

反映していることを示している。

以上の結果に基づき、乾燥サイトのアカマツの約 100 年分の年輪を早材、晩材に切り分け、降水量および気温との比較を行った。晩材の炭素同位体比と 7 月の降水量との間に有意な相関が見られた。このことは、年輪幅と密度に加え、炭素安定同位体比を測定することにより、東シベリアタイガ林の水分環境を復元できる可能性を示している。

上記のとおり、本論文はこれまで研究が進んでいない東シベリアタイガ林樹木の炭素安定同位体シグナルがどのような過程を経て記録されているか、そして同位体年輪気候学にどのように応用しうるかを示したもので、古環境復元のための生理学的基礎を確立したと言える。実際の古環境復元には狭い年輪幅を切り分けるという技術的な課題が残されており、実現には至っていないが、本論文で示された年輪形成過程までのプロセスをふまえた解析は、大きな季節性を有する環境の復元を可能にする成果である。