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学 位 論 文 題 名

Chemo-ecophysiological study on growth and defense responses of the afforestation species eucalypt and acacia under a changing environment

（変動環境下におけるユーカリとアカシア類の成長と防御機構に関する生態生理化学的研究）

学位論文内容の要旨

Introduction

Afforestation efforts are assigned by many nations and stakeholders to moderate the living environment and to contribute to the sustainable production of forest resources. Acacias and eucalypts are among the pioneer species suitable for afforestation in sub-tropical and tropical regions where growing environment has been changing drastically. These trees have been widely planted because of their fast growth and their adaptability to diverse growth conditions; however, their chemo-ecophysiological capability needs further investigations in term of adaptation to the changing environment in the future.

In general, plants growth is restricted to some extent by extreme physical environmental factors, e.g. high temperature, high soil nitrogen (N) level, high atmospheric [CO_2] as well as high concentration of air pollutants such as tropospheric O_3. However, plant responses to the changing environment greatly vary and depend on heredity and other environmental limitations. Therefore, the performance of eucalypt and acacia in the changing environment is defined by their ability to exploit and allocate resources originated from photosynthesis to maximize growth.

The general concern underlying this research is the chemo-ecophysiological responses of eucalypts and acacias to high atmospheric [CO_2], [O_3] and nitrogen deposition, to cope with future climate change as they will be used as promising materials for afforestation. I examined the responses of these species to high level of [CO_2], [O_3], and nitrogen loading. I conducted some experiments to elucidate the issues and present the results in six parts: 1) Ecology of eucalypts and acacias, 2) Nitrogen deposition and ozone in East Asia, 3) The effect of N deposition on photosynthetic, growth, and leaf traits of eucalypts and acacia, 4) Chemo-ecophysiological responses of eucalypts under elevated [CO_2] and high N load, 5) Photosynthetic, growth, and defense responses of eucalypts under elevated [CO_2] and [O_3], and 6) General discussion.

1. Ecology and silviculture of the eucalypts and the acacias

I summarize the growth traits of the vegetation in the native localities, their habitat, plantation performance, and the commercial importance of eucalypts and acacias in the future.

2. Nitrogen deposition and ozone in east Asia

Rapid changes in atmospheric condition, such as increasing [SO_x], [NO_x], [O_3], and [CO_2] represent critical issues to afforestation. For this study I collect information from literatures and did field surveys in their plantations in Indonesia and Taiwan.

For measurement of gases concentration, a Passive Sampler Method (Ogawa & Co. USA, Inc) was used.

[O_3] in Indonesia sites and Taiwan sites were relatively similar which was remaining below the standards threshold in Indonesia. The [NO_x], [NO_2], and [NO] were higher in Indonesia sites than in Taiwan's because of the study site-effect. (Literatures surveys are on-going).

3. Photosynthetic, growth, and leaf traits of eucalypts and acacias under high N load

Photosynthetic nitrogen and water use efficiency (PNUE and WUE) of eucalypts and acacias should be considered on selecting seedlings regarding the afforestation site's condition. These factors may capable to predict how net photosynthetic capacity is optimized per unit of water and nitrogen in leaves.

Eucalyptus urophylla, *E. grandis*, *E. nitens*, *Acacia mangium*, and *A. auriculiformis* were grown in 7 l pots with Kanuma pumice and clay soil (1:1, v/v). Four levels of $(NH_4)_2SO_4$ were designated to supply N at 0, 25, 50 and 100 kg ha^{-1} yr^{-1}.

Nitrogen (N) deposition to some extent may improve the photosynthetic and growth traits of the eucalypts and acacias. However, N input level to environment should be considered, because too high N level might give inefficient result. Apparently, high N load improved the photosynthetic traits of the acacias better than that of the eucalypts, because the PNUE of the acacias increased by high N load and the A_{growth} could surpassed that of the eucalypts. Little evidence was found on the effect of N load to the WUE of both genera in this study.

4. Chemo-ecophysiological responses of eucalypts under elevated [CO_2] and high N load

In general, photosynthetic rate and growth of plant increase under elevated [CO_2] and high soil N condition. In this study, I studied the performance of two eucalypt species under the interaction of elevated [CO_2] and high N to comprehend their suitability as materials for afforestation in the condition simulating the future environment with high N deposition and elevated atmospheric [CO_2].

E. urophylla and hybrid *E. camaldulensis* x *E. deglupta* were grown in 7 l pots with Kanuma pumice and clay soil (1:1, v/v) in phytotron chambers under natural light condition equipped with supplemental light to simulate day length in their native habitat. The seedlings were subjected to two levels of [CO_2] (380 and 760 μmol mol^{-1}) and two levels of N (0 and 50 kg ha^{-1}).

The photosynthetic rate was increased by both high N load and elevated [CO_2], but only high N pronouncedly enhanced the growth of the eucalypts. When N was not a limiting factor, A_{growth} increased under elevated [CO_2]. A trade-off of resource allocation was apparent between growth and secondary metabolites concentration under both elevated [CO_2] and high N load.

5. Photosynthetic, growth, and defense responses of eucalypts under elevated [CO_2] and [O_3]

The availability of N and C influences plant leaf chemistry, which in turn would define plant defense status. Increasing the availability of these resources may induce changes not only in plant growth traits but also in plant defense strategies. At high [CO_2], stomatal conductance decrease to reduce the ozone absorption. Many studies have reported that high [CO_2] moderates the SM that is altered by high [O_3], because exposure to [O_3] alters the leaf chemistry because ozone is considered as an abiotic elicitor of plant defense reaction. Elevated [CO_2] is also possibly to ameliorate the effect of harmful ozone.

E. globulus, *E. grandis*, and hybrid *E. camaldulensis* x *E. deglupta* were grown in Open Top chambers (OTCs) in the nursery. The seedlings were subjected to two levels of [CO_2] (ambient and 600 ppm) during daytime and two levels of [O_3] (<10 and 60 ppb) for 7 h during daytime.

Condensed tannins tended to increase under elevated [CO_2] that may related to either a trade-off with the retarded-growth or the increase in resources availability for SM production. Photosynthetic and growth traits of the eucalypts seemed irresponsive to high [O_3] as compared to high [CO_2]. However, GC profiles of leaf extract showed that elevated [O_3] and [CO_2] marginally increased the concentration of a particular compound, also the possibly ameliorating effect of high [CO_2] on the effect of [O_3]. (The identification and structure elucidation of the compound will be conducted in the near future).

General Discussion

Less evidences were found on nutrient, especially nitrogen, interfered the impact of elevated [CO_2], although nutrients significantly improved the net photosynthetic and growth rate of the eucalypts and the acacia. The improvement on net photosynthetic and growth rate was less pronounced by elevated [CO_2]. Although the photosynthetic rate tended to decreased slightly, there was no significant reduction in photosynthesis and growth of the eucalypts by elevated [O_3]. Based on these findings, therefore, acacia and eucalypts can be considered as afforestation species under the rapidly changing environment.

学位論文審査の要旨

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本論文は、図27、表10、引用文献179編からなる全111ページの英文論文である。参考論文4編が添えられている。

植林は木質資源の持続的有効利用だけではなく生活環境を維持するためにも重要な位置づけにある。特に、熱帯・亜熱帯地域は木質資源の有望な生産場所であるだけではなく地球環境に大きな影響をもたらす。これらの地域の有力な植栽樹種としてアカシア類とユーカリ類がある。さまざまな角度から、これらの樹種の成長特性が調べられてきた。しかし、オーストラリア以外の地域ではユーカリ類には虫害などがほとんど見られず、虫害に対する防衛機構には情報が限られているのが現状である。

産業革命以来、大気中のCO_2濃度は上昇し続け、増加速度が従来までの1.5 ppm/年から、この10年間では2.0 ppm/年に達し、窒素沈着量も急激に増加してきた。さらに、近年、強力な酸化物質であるオゾン濃度が急上昇し、越境大気汚染の可能性が指摘されており、この傾向はアジア地域全体にも拡大することが懸念される。このように生産環境が激変する中で、主要な造林樹種であるアカシア類とユーカリ類の成長と虫害等に対する防御に注目して、成長と防衛機構を解明することを目的に研究を行った。

ここで、広葉樹では成長に直結するリグニン生産とタンニンなどの被食防衛物質はフェニールアラニンから誘導されるため、生化学的トレードオフが存在する。これら二次代謝産物は光合成産物の最終産物であるが、これらの割合が急激な環境変化下でどのように変化するのかを解明した。

第一章では、研究の背景、対象としたアカシア類とユーカリ類、現在の大気環境の変化との関連を概説し、貧栄養下では被食防衛機能が向上するという仮説を建てた。第二章では、窒素沈着を中心としてオゾンや硫黄酸化物の現状を台湾中部とインドネシア・ジャカルタ近郊にて、一時期ではあるがパッシブサンプラー法を用いた調査を行った。その結果、東京の濃度60 ppb以下の状況であることが示唆された。第三章ではアカシア類二種（*Acacia mangium*, *A. auriculiformis*）とユーカリ類三種（*Eucalyptus urophylla*, *E. grandis*, *E. nitens*）を対象に光合成作用に関連した水、窒素利用を調べた。この結果、水利用には窒素沈着の影響はあまり見られなかったが、アカシア類は窒素利用効率がユーカリ類に比べて低かった。これらの知見から個葉レベルからみた植栽可能な立地の基礎情報を提供できた。

第四章では、進行し続ける大気中CO_2濃度と窒素沈着の複合影響について人工気象室を利用して調べた。*E. urophylla*と雑種 *E. camaldulensis* x *E. deglupta*の小型苗を用いたポット材料を380 ppmと760 ppmと窒素量0 kg/ha年と50 kg/ha年の組み合わせ処理で半年育成した。光合成速度は高CO_2・窒素条件で増加したが、窒素が多い環境でのみ成長量が増加した。また、リグニン量と成長とフェノール性の防衛物質の量にはトレードオフ関係が認められた。

第五章では高CO_2とオゾン(60 ppb：日中6時間)処理の影響を調べた。予想したことは高CO_2では気孔が閉じ気味になるので、有害物質であるオゾンの取り込みが減少することである。対象としたのはユーカリ樹3種（*E. globulus*、*E. grandis*、雑種 *E. camaldulensis* x *E. deglupta*）であった。天井の開いたオープントップチェンバーを用いてCO_2濃度（380 ppmと600 ppm）とオゾン（活性炭で一度オゾンを除去し、そこへオゾンを付加）は0 ppbと60 ppb (6時間)とした。この結果、約半年間での伸長・肥大成長に明確な差は見られなかったが、特に、*E. globulus*と雑種ではリグニン量が高CO_2で増加傾向を示した。一方、期待した高CO_2での気孔閉鎖によるオゾンの吸収抑制効果は不明瞭であった。しかし、葉のメタノール抽出物のガククロマトグラフィーと質量分析の結果、オゾン処理ではエピクチクラワックスの主要成分である*n*-エイコサンの増加が見られ　その相対値は高CO_2では少ない傾向が雑種に見られた。この物質は防御に関して何らかの調節作用を持つと考えられる。

増加し続ける大気CO_2濃度は、窒素を中心に土壌の栄養条件が劇的に改善されないなら光合成の「負の制御」をもたらす傾向のあることがわかった。オゾンに対しては、東京で日中観測される濃度であっても二次代謝産物の生産には影響があることがわかった。これらは虫害などの発生予測につながる内容と考えられる。本研究の知見は変動環境での植林に重要な森林保護の基礎的知見を与える。よって、審査員一同は、Novriyanti Ekaが博士（農学）の学位を受けるのに十分な資格を有するものと認めた。