

Impacts of natural disturbances on forest carbon sequestration: Perspectives from frequent typhoons and prolonged intensive deer herbivory

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Impacts of natural disturbances on forest carbon sequestration: Perspectives from frequent typhoons and prolonged intensive deer herbivory

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submitted to the Graduate School of Bioresource and Bioenvironmental
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要旨

森林による炭素隔離は気候変動下で森林に期待される公益的機能のひとつである。本機能は 1) 生態系内に蓄積される炭素量と、2) 正味の炭素吸収量の 2 点から評価される。正味の炭素吸収量は純一次生産による炭素吸収から、従属栄養呼吸による CO_2 放出を差し引いて求める純生態系生産 (Net ecosystem production; NEP) や、NEP に加え土壌侵食などその他の炭素の移出入を考慮した純生態系炭素収支 (Net ecosystem carbon balance; NECB) として推定される。これらは、生態系の構造を改変する自然撓乱によって変動する。多くの既往研究において、自然撓乱が森林の炭素隔離機能に及ぼす影響は、火災や病虫害のまん延など、稀に起こる単一の撓乱を対象に評価されてきた。このような単発の撓乱の場合、上層木の枯死に伴い炭素隔離機能は一時的に低下するが、その後の植生更新を通じて回復することが数多く報告されている。一方で、頻発・継続する撓乱が森林の炭素隔離機能に及ぼす影響については研究例が乏しい。こうした知見の不足は、気候変動や人間活動の変化に伴い、自然撓乱の頻発化・長期継続化が懸念されるなかで、炭素隔離機能の現状及び将来評価に不確実性をもたらしている。そこで本論文では、自然撓乱が頻発・継続するケースにおける炭素隔離機能の変化を理解することを目的とした。本論文は序論 (第 1 章) と結論 (第 6 章) を含む全 6 章で構成される。第 2 章と第 3 章では頻発する撓乱として、沖縄島北部で繰り返し生じる台風を、第 4 章と第 5 章では継続する撓乱として、九州島南部で 1980 年台から続くシカによる強度な植生採食を対象とし、各撓乱が炭素隔離機能に及ぼす影響を野外計測に基づき評価した。

第 2 章では沖縄島北部の亜熱帯常緑広葉樹林に対し、頻発する台風が与える影響を評価した。本地域では台風に伴い幹折れや樹木枯死が観察されていることから、台風は枯死木など粗大木質有機物 (Coarse woody debris; CWD) の生産を通じて炭素隔離機能に影響すると考えられる。このため、まず本地域内にある 2500 m^2 の調査プロットで 2013, 2016, 2019 年に得られた毎木調査データ (樹種・樹高・胸高直径) を解析し、林分の動態と CWD 生産の関係を調べた。その結果、本林分の CWD 生産量は $130.4 \pm 33.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ と推定され、これは上層木の幹バイオマスの年間蓄積量 ($150.0 \pm 7.1 \text{ g C m}^{-2} \text{ yr}^{-1}$) に匹敵した。また、幹バイオマスは 2013 年 ($7067.3 \text{ g C m}^{-2}$) から 2019 年 ($7184.7 \text{ g C m}^{-2}$) にかけてほとんど変化しなかった。CWD 生産に対する樹種・樹木サイズ・地形・林分密度の影響を調べたところ、特に樹高の高い個体ほど、CWD 生産確率が高かった。従って、主に風に曝されやすい樹木個体の幹折れと枯死によって、本林分では CWD が多量に生産され、かつ幹バイオマスの蓄積が制限されていることが示唆された。続く第 3 章では、同林分で落葉・落枝・CWD を含む枯死有機物の現存量と CO_2 放出量を計測した。その結果、CWD は枯死有機物全体の現存量 ($1499.7 \text{ g C m}^{-2}$) の約 78%、 CO_2 放出量 ($340.6 \text{ g C m}^{-2} \text{ yr}^{-1}$) の約 45% を占めた。CWD からの CO_2 放出量 ($153.7 \text{ g C m}^{-2} \text{ yr}^{-1}$) は CWD 生産量と同程度であり、本林分では CWD が多量に供給されるが、同程度の炭素が CWD から放出されていることを示唆した。本研究で得られた結果に加え、既往研究のデータにより推定された本林分の NEP は $-346 \text{ g C m}^{-2} \text{ yr}^{-1}$ となり、正味の炭素放出源であると考えられた。これは、東アジアの亜熱帯林が一般的に正味の炭素吸収源 (平均 NEP = $362 \text{ g C m}^{-2} \text{ yr}^{-1}$) であるとする先行研究とは対照的な結果であった。

第 4 章では継続する強度なシカの採食が九州島南部の冷温帯針広混交林に及ぼす影響を評価した。本地域では個体数の増加したシカの採食に伴い 2000 年前後に下層植生が

消失し、下層植生のある林分(Presence of understory; PU)の多くが下層植生の消失した林分(No understory; NU)に変化した。NUの一部はさらに、ギャップを含む疎林(Canopy gap; CG)や不嗜好性種のアセビ優占林(Shrublands; SR)への移行が観察されている。また PU から NU への移行に伴い、土壌侵食によって樹木根が地上に露出するほど土壌層が剥離している。そこでまず、根の露出が樹木成長に与える影響を調べたところ、同一林分内のブナ成木 12 個体の間で、根の露出程度を定量化した指標が大きいほど、個体レベルの葉生産量及び幹の肥大成長量が小さいことが分かった。各個体の年輪幅と、年輪木部の炭素安定同位体の分析から、肥大成長の低下は下層植生の消失時期から生じており、それは水利用効率の増加(水ストレスの増加)を伴うことが分かった。これらから、土壌侵食は樹木根の露出に伴う水欠乏によって樹木衰退を引き起こすことが示された。またこの樹木衰退は、NU から SR、CG への移行を促進する一因となっていると推測された。続く第 5 章では、PU から NU・SR・CG への変化に伴う炭素隔離機能の変化を明らかにするために、各林分タイプで 100-400 m² の調査プロットを 4 反復設置し、地上と地下の総炭素蓄積量、並びに NECB を推定した。PU における地上と地下の総炭素蓄積量($25190.5 \pm 3065.1 \text{ g C m}^{-2}$)を基準とすると、PU から NU($20683.6 \pm 4152.2 \text{ g C m}^{-2}$)、SR($14162.5 \pm 6561.1 \text{ g C m}^{-2}$)、CG ($12953.1 \pm 6160.3 \text{ g C m}^{-2}$)への変化は、総炭素蓄積量を最大 50%低下させると考えられた。NECB を推定した結果、PU($307.0 \pm 244.6 \text{ g C m}^{-2} \text{ yr}^{-1}$)および SR($92.3 \pm 158.1 \text{ g C m}^{-2} \text{ yr}^{-1}$)は正味の炭素吸収源であったのに対し、NU($-98.2 \pm 92.3 \text{ g C m}^{-2} \text{ yr}^{-1}$)及び CG ($-894.4 \pm 442 \text{ g C m}^{-2} \text{ yr}^{-1}$)は正味の排出源であった。NECB が低下した主要因は、シカの採食に伴い後継樹が不足したことによる林分全体の一次生産量低下、樹木衰退に起因する多量の CWD からの CO₂ 放出、及び土壌侵食による土壌有機物の流亡であった。このような NECB の低下が、炭素蓄積量の低下を引き起こした。

第 6 章では以上の結果をまとめ、頻発・継続する攪乱が炭素隔離機能に与える影響について総括した。本論文では、頻発・継続する攪乱は、いずれも樹木衰退と枯死を引き起こし、その結果、純一次生産の減少、CWD 生産の増加、及び土壌侵食による炭素の系外流出などを介して正味の炭素吸収量を低下させ、最終的に林分の炭素蓄積量を制限ないし減少させることを示した。本研究で示された炭素隔離機能の劣化は、これまで研究されてきた単発の攪乱に関するケースと同程度であったが、攪乱が頻発・継続する限り機能の回復が見込めないという点で、単発の攪乱よりも長期的な機能劣化をもたらすと考えられた。沖縄島北部の森林では、現状では高い炭素隔離機能は期待できないため、本機能を増強するのであれば、人為的介入を含む積極的な管理の検討が必要であることが示唆された。また九州島南部の森林では、シカの植生採食後に生じる土壌侵食が樹木の衰退と土壌炭素の流亡を加速させることから、防鹿柵の設置を通じて下層植生を保全することが、将来的な炭素隔離機能の劣化抑制に有効であると考えられた。将来的な攪乱の頻発化・長期継続化は多くの林地で炭素隔離機能を劣化させると考えられるため、今後様々な林地において本機能を評価し、劣化の著しい場所においては早急に緩和策を講じる必要があると考えられる。

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Lists of manuscript

The dissertation consists of six chapters. Chapters 1, 2, and 6 were newly written for this dissertation. Chapters 3 and 4 were written based on the published as peer-reviewed papers. Chapter 5 includes parts that have been newly written for this dissertation, in addition to published papers. existing papers. The list of manuscripts are as follows:

Chapter 3

Hayato Abe, Ayumi Katayama, Shingo Taniguchi, Atsushi Takashima, Tomonori Kume, Kazuho Matsumoto (2022) Effects of differences in aboveground dead organic matter types on the stand-scale necromass and CO₂ efflux estimates in a subtropical forest in Okinawa Island, Japan. *Ecological Research*, 37 (5), 609-622. <https://doi.org/10.1111/1440-1703.12317>

Chapter 4

Hayato Abe, Tomonori Kume, Fujio Hyodo, Mimori Oyamada, Ayumi Katayama (2024) Soil erosion under forest hampers beech growth: Impacts of understory vegetation degradation by sika deer. *Catena*, 234, 107559. <https://doi.org/10.1016/j.catena.2023.107559>

Chapter 5

Hayato Abe, Tomonori Kume, Ayumi Katayama (2024) Reduction in forest carbon stocks by sika deer-induced stand structural alterations. *Forest Ecology and Management*, 562, 121938. <https://doi.org/10.1016/j.foreco.2024.121938>

Hayato Abe, Tomonori Kume, Ayumi Katayama (2024) Sensitivities of soil respiration and heterotrophic respiration to temperature in a cool-temperate forest with sika deer-induced understory vegetation alteration [preprint]. *EarthArXiv*, Submitted to *Journal of Agricultural Meteorology* (In major revision). <https://doi.org/10.31223/X5KH64>.

Statement of originality and contributions

The author of this dissertation, Hayato Abe, declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this dissertation. This dissertation has never been submitted, in the same or similar form, to another examination commission for a degree. Chapters 1, 2, and 6 contain no material previously published or written by another person. Chapters 3–5 were written based on above mentioned lists of manuscripts. For this reason, this dissertation uses “we” rather than “I” as the first person. In chapters 2–5, Hayato Abe has contributed to the conceptualization, methodology, formal analysis, investigation (i.e., field measurement, sample collection, and laboratory analysis) from 2019 to 2024, the resources, data curation, visualization, and the writing-original draft in manuscripts. Chapter 2 includes analyses that use data obtained by the Laboratory of Silviculture at the University of the Ryukyus from 2013 to 2019; Hayato Abe contributed to this data collection in 2019.

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Chapter 1: General Introduction

1.1. The role of forest ecosystems under global warming

Global warming, the long-term increase in Earth's surface temperature, is one of the most urgent challenges facing humanity (IPCC 2023). Global warming is primarily driven by human-induced greenhouse gases (GHGs) emissions such as carbon dioxide (CO₂) and methane (CH₄) (Fuss et al. 2018). GHGs trap infrared radiation that Earth emits into space, with part of this energy being re-radiated back to Earth's surface, thereby increasing temperature (Manabe and Wetherald 1967). Among GHGs, CO₂ plays a central role due to its abundance and longevity in the atmosphere (Friedlingstein et al., 2014). The current global CO₂ emission is about 11 Pg C yr⁻¹, and approximately 90% of this is from the combustion of fossil fuels (Friedlingstein et al. 2023). Given the difficulty of eliminating all fossil fuel combustions (Fuss et al. 2018), it is necessary to promote carbon (C) absorption to compensate for this.

While various artificial- and nature-based solutions for CO₂ capturing are being proposed, much attention is still being paid to forest C sequestration (FCS) (Siry et al. 2005; Fuss et al. 2018). Forest ecosystems cover about 3.8 billion ha, i.e., 30% of the world's land area (FAO 2020). It is predicted that the current world's forest stores approximately 870 Pg C (Pan et al. 2024). Over the past several decades, this C stocks have consistently increased by net absorption of about 3.5 Pg C yr⁻¹ (i.e., 20–30% of global CO₂ emissions) (Harris et al. 2021; Pan et al. 2024). In addition, forest management practices, including afforestation, reforestation, and restoration, are believed to maintain and enhance current FCS until it recaptures the 180 Pg C—the amount of C loss from forests through past land-use changes (Fuss et al. 2018; Walker et al. 2022; Chand et al. 2022; Roebroek et al. 2023; Pan et al. 2024). The FCS is achieved through vegetation absorbing CO₂ and producing organic matter, which is then stored in various above- and below-ground components as reservoirs. Thus, FCS is evaluated from two perspectives: the amount of C stocks in the ecosystem and the amount of net C absorption.

1.2. Brief explanation of forest carbon cycling

1.2.1. Carbon stock components

Forest C stocks are expressed as the weight of C per unit area (g C m^{-2}). Forest C stocks involve various components (Fig. 1-1). These C components can be classified by above-ground C stock (AGC) and below-ground C stocks (BGC). AGC includes living vegetation (overstory trees and understory vegetation) and above-ground dead organic matter (DOM). Above-ground DOM comprises leaf litter, fine woody debris (FWD), and coarse woody debris (CWD). Leaf litter and FWD are collectively referred to as surface litter. BGC includes coarse roots, fine roots, below-ground DOM, and soil organic matter (SOM). Although the criterion for separating these components differs depending on the research, the following criteria will be used in this dissertation. Overstory trees were defined as living trees with a height >2 m. Understory vegetation was defined as living plants without overstory trees, including tree seedlings with a height <2 m, dwarf bamboo, mosses, ferns, and other herbs (Deng et al. 2023). CWD was defined as woody debris with a central diameter ≥ 3 cm (Harmon et al. 1986). FWD was defined as woody debris with a diameter of <3 cm and without fragmented woody organ particles with approximately <5 mm diameter. Fine roots included all living plant roots with a diameter < 2 mm (McCormack et al. 2015). The coarse roots included overstory tree roots without fine roots. SOM included organic matter in mineral soils without leaf litter or FWD (Weber 2002). Note that, unless otherwise specified, the above definitions will be used consistently throughout this dissertation.

1.2.2. Carbon fluxes

Net C absorption is often evaluated as increased C stocks over a year ($\text{g C m}^{-2} \text{yr}^{-1}$). This is also referred to as the net ecosystem C balance (NECB) when focusing on the path of C moving in and out of the system (i.e., flux). NECB is calculated as follows (Chapin III et al., 2006) (Fig. 1-2):

$$B = E \pm O = P_n - R_h \pm O \quad (\text{Eq. 1-1}),$$

where B is NECB, E is net ecosystem production (NEP), P_n is net primary production (NPP), R_h is heterotrophic respiration (HR), and O is other C transfer (OT) between systems. A positive value for NECB indicates the accumulation of C in the ecosystem, while a negative value indicates C loss from the ecosystem. NEP was defined as the CO_2 exchange between the

atmosphere and ecosystem, calculated by NPP and HR. The NPP is defined as the released CO₂ by vegetation respiration (autotrophic respiration, AR), subtracted from absorbed CO₂ by vegetation photosynthesis (gross primary production, GPP). The NPP can be estimated using biometric methods as follows (Ohtsuka et al. 2016):

$$P_n = I_o + I_u + L + R_f \quad (\text{Eq. 1-2}),$$

where I_o is the stand increments of overstory woody biomass, I_u is the stand increments of aboveground understory biomass, L is aboveground production of leaf litter and FWD, and R_f is fine root production. The HR express the CO₂ efflux from DOM and SOM:

$$R_h = R_{h_DOM} + R_{h_SOM} = R_{h_LL} + R_{h_FWD} + R_{h_CWD} + R_{h_SOM} \quad (\text{Eq. 1-3}),$$

where R_{h_DOM} , R_{h_SOM} , R_{h_LL} , R_{h_FWD} , and R_{h_CWD} are CO₂ efflux from DOM, SOM, leaf litter, FWD, and CWD, respectively. The OT includes three types of C fluxes: (1) uptake and release of C-included gaseous other than CO₂ such as CH₄, (2) movement of dissolved inorganic and organic C, and (3) lateral transfer of non-gaseous and non-dissolved particulate such as SOM loss due to soil erosion. These OT are recorded as positive values when entering the ecosystem from the outside, and as negative values when leaving outside from the ecosystem. Note that fragmentation of DOM (Berg and McClaugherty 2003) is not included in OT because these processes are the transition of components from CWD to FWD and from FWD to SOM.

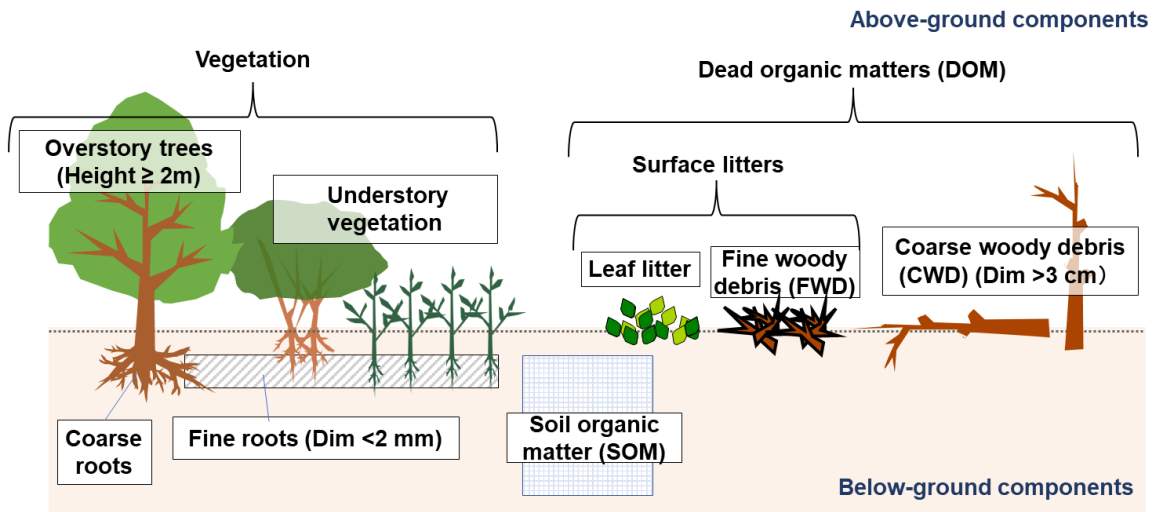


Fig. 1-1. Diagram of major forest carbon stock components

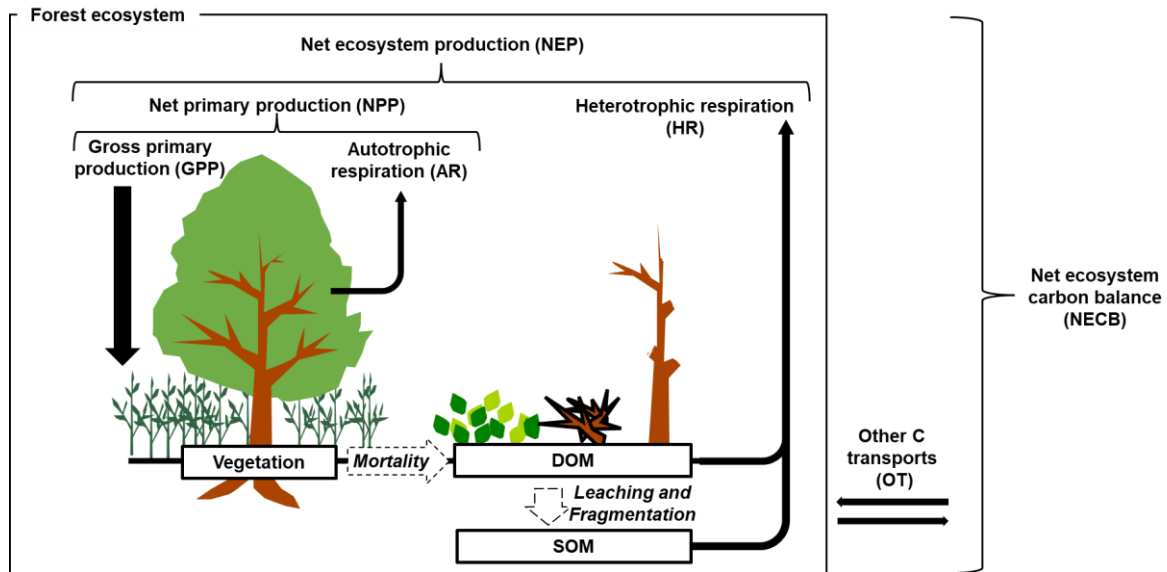


Fig. 1-2. Conceptual diagram of net ecosystem carbon balance fluxes in forest

1.3. The effect of natural disturbance on forest carbon sequestration

1.3.1. Single pulse disturbance

Except for anthropogenic interventions such as logging, the FCS is affected by natural disturbance, which is the drastic phenomenon that alters vegetation recruitment, growth, and/or death over a wider area (Grubb 1977; Hicke et al. 2012). There are various definitions of disturbance, which target different components of ecosystems and different times and spaces. In the earliest studies of natural disturbance and FCS, natural disturbance was defined as “mechanisms which limit the plant biomass by causing its partial or total destruction” (Grime, 1979) (Table 1-1). Since then, the definition of natural disturbance has been modified depending on the target FCS and spatiotemporal scale (Table 1-1). Currently, one of the well-used definitions is that of White and Pickett (1985): “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability of the physical environment” (Jentsch and White 2019; Sturtevant and Fortin 2021). As this definition suggests, studies of natural disturbance on FCS have primarily focused on discrete events that occur over a short period and result in the immediate decline and death of trees, such as fire, drought, windfall, and the spread of pests and diseases (McCarthy 2004;

Seidl et al. 2017). In this dissertation, such natural disturbances are called single pulse disturbance (SPLD) (Bender et al., 1984) to emphasize their temporal characteristics to distinguish it from the other types of natural disturbance described later (see section 1.3.2).

Table 1-1. Definitions of natural disturbance often used in research on forest carbon sequestration study

Reference	Definition
Grime (1979)	Mechanisms that limit the plant biomass by causing its partial or total destruction.
Bazzaz (1984)	Sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response
White and Pickett (1985)	Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability of the physical environment.
Pickett et al. (1989)	A set of events that can disrupt any ecological level, environmental, component as well as the organizational status of a biological cycle of organisms
Seidl et al. (2011)	A discrete event in time that disrupts ecosystem structure, composition and/or processes by altering its physical environment and/or resources, causing destruction of plant biomass
This dissertation	Series of events that disrupt ecosystem structure and related environmental conditions, affecting forest carbon sequestration

The impact of SPLD on FCS has been well-documented through numerous field surveys (Seidl et al. 2017). The findings have been integrated based on the ecological framework of vegetation demography (Goulden et al. 2011). In this framework, FCS is temporally changed with SPLD-induced alterations in recruitment, growth, and mortality. The typical trajectory is as follows. Following an SPLD, many overstory trees in the stand decline and die (Jentsch and White 2019). Afterward, overstory trees will either recover or successional trees will grow to replace them, and the stand will be regenerated to its pre-SPLD state (Harmon et al. 2020). Regarding FCS, the mortality of trees can be understood as a transfer of components from overstory trees into CWD. Thus, SPLD temporarily altered the stand to a net C source (i.e., showing a negative value of NECB), mainly due to decreased NPP from the overstory trees and increased HR from CWD (Harmon et al. 2011). This degraded FCS is finally offset over time

because of increased NPP via the growth of new recruitment or remaining vegetation and decreased HR from CWD via reductions of CWD stocks (Harmon et al. 2011). Therefore, forest C stocks decrease initially after SPLD and return to pre-SPLD level as the forest regenerates (Hicke et al. 2012).

1.3.2. Multiple pulse disturbances and press disturbances

Natural disturbances occur not only as a single-discrete event (i.e., SPLD) but also multiple times or continuously. Previously, Bender et al. (1984) defined disturbances that occur continuously as press disturbances (PRD) and separated it from SPLD. Similarly, Inamine et al. (2022) called disturbances that occur repeatedly as multiple pulse disturbances (MPLD). However, compared to SPLD, there were relatively few documents on the impact of MPLD and PRD on FCS because these disturbance types deviate from the classical view of natural disturbance, such as a temporally discrete event (Williams et al. 2016) (Table 1-1). Here, this dissertation defines natural disturbances as a “Series of events that disrupt ecosystem structure and related environmental conditions, affecting forest carbon sequestration” (Table 1-1). The detailed explanation of SPLD, MPLD, and PRD are described in supplemental sections S1.1. to S1.4. in this chapter.

As described in supplemental section in this chapter, vegetation demography is the key feature separating SPLD, MPLD, and PRD based on their ecological impacts. MPLD and PRD may not always follow the same trajectory of FCS degradation and subsequent recovery as SPLD. The FCS degradation against and subsequent recovery against SPLD (section 1.3.1.) demonstrate that the vegetation tends to reorganize to its original state after being disturbed. This reorganization pattern is called resilience (Seidl and Turner, 2022). In contrast, field observations reported that MPLD and PRD leads to a different vegetation state after disturbance (Scheffer and Carpenter 2003). Seidl and Turner (2022) proposed three types of non-resilient reorganization patterns, namely restructuring, reassembly, and replacement, by focusing on stand structure and species composition. Restructuring refers to the vegetation recovery with changes in stand structure, such as tree height and its variation. Reassembly refers to vegetation recovery with changes in species composition. Replacement refers to vegetation recovery with changes in both stand structure and species composition. For example, prolonged drought (PRD) regulates regrowth in conifer forests, resulting in shorter canopy height compared to the pre-drought state (i.e., restructuring) (McDowell et al. 2020; Batllori et al. 2020). Repeated fire

(MPLD) promotes the transition from spruce (*Picea mariana*) forests to broadleaved or pine (*Pinus banksiana*) forests (i.e., reassembly) (Johnstone et al. 2016, 2020). Repeated fire (MPLD) and prolonged soil erosion (PRD) promote the transition from broadleaved forests to open canopy areas with a mixture of shrub and grass species (i.e., replacement) (Flores et al. 2020). These non-resilient reorganization processes suggest the possibility that vegetation biomass does not return to its original level after MPLD and PRD (Pan et al. 2024).

Reflecting these non-resilient reorganizations and related degradation of vegetation biomass, many review papers stated that MPLD and PRD would degrade forest C stocks and/or NECB (Paine et al. 1998; Flores et al. 2020; Burton et al. 2020; Albrich et al. 2020; Sturtevant and Fortin 2021). For example, continuous drought has been reported to shift the system to a long-term net C source because lower NPP in the reorganized stand cannot offset the increased HR from CWD (Williams et al. 2016). Similarly, in areas where frequent snow avalanches occur, it has been reported that the forest C stocks are permanently reduced because the regenerated vegetation and SOM are repeatedly discharged out of the system (Vacchiano et al. 2015). Nevertheless, comprehensive evaluations of forest C stocks and NECB with consideration of the increment of HR from CWD and OT such as SOM loss by erosion have rarely been conducted for MPLD and PRD (Kleinman et al. 2019; Albrich et al. 2020). This knowledge gap is hindering the decision as to whether forest restoration programs are necessary for MPLD and PRD and is also impeding the development of management techniques and the identification of priority restoration areas when they are needed (Führer 2000; Lindner et al. 2010, 2014; Keenan 2015; van Lierop et al. 2015; Ghazoul et al. 2015). Therefore, conducting field studies regarding MPLD and PRD is crucial, especially in addressing the following questions. (1) To what extent do MPLD and PRD cause reductions in forest C stocks and NECB? (2) How do MPLD and PRD lead to reductions in forest C stocks and NECB? (3) Where are the reductions in forest C stocks and NECB most pronounced within the stand and/or landscape?

1.4. Frequent typhoons and deer overbrowsing: recent concerning disturbances

Globally, it is predicted that MPLD and PRD will increase due to the rising frequency and

duration of natural disturbances associated with global warming and changes in human activity (Andersen et al. 2009; Rocha et al. 2018; Blowes et al. 2019; Thomas 2020; McDowell et al. 2020; Senf and Seidl 2021). In the northern hemisphere, two such examples are the increase in the frequency of tropical cyclones (TCs), which leads to MPLD, and the overpopulation of ungulates, which leads to PRD. These disturbances are considered particularly suitable as a first step to deepening our basic and empirical understanding of the impact of MPLD and PRD on FCS for the following three reasons. First, the frequency and duration of these disturbances can be identified from literatures, making easily to discuss their impact on FCS. Second, the driver of each disturbance is different (i.e., physical and biotic disturbances), altering stand structure via different vegetation demographic processes; hence, it is possible to consider the universality and diversity of patterns of FCS degradation. Third, empirical evidence regarding their impacts on FCS are required because these disturbances are occurring in areas of interest for forest management, or in areas where there is a clear need for forest management strategies to deal with disturbances.

TCs, such as hurricanes and typhoons, are large-scale wind gusts that primarily affect islands and coastal areas (Ibanez et al. 2019, 2024). Annually, 74–90 TCs with wind speeds exceeding 35 knots ($= 18 \text{ m s}^{-1}$) are generated near the equator (Schreck et al. 2014; Sobel et al. 2021). The majority of these TCs move into the Northern Hemisphere (about 70% of total TCs), particularly toward East Asia (about 30%) (Schreck et al. 2014; Sobel et al. 2021). Consequently, Asian forests in islands and coastal areas are regularly impacted via TCs (Mitchell 2013; Ibanez et al. 2019). Because forests in these areas are expected to be high C sink (Yu et al., 2004), evaluating the impact of TC is important when considering management for these areas. Generally, a single TC in this area can be recognized as SPLD (Buma 2015). Single TC can instantly cause stem breakage and mortality, producing CWD (Gardiner et al. 2016; Ibanez et al. 2019). At the same time, canopy openings caused by the TC can promote the recruitment and growth of surviving trees (Uriarte et al. 2004, 2009; Gardiner et al. 2016). However, in recent decades, rising sea surface temperatures due to global warming have been shown to increase the frequency of intense TCs (Pielke et al. 2005; Mann and Emanuel 2006; Moon et al. 2019; Kossin et al. 2020). For instance, in Japan, the return period for TCs with wind speeds of around 45 m s^{-1} is projected to change from 100 years to 10 years (Bloemendaal et al. 2022). Such frequent TCs are considered MPLD (Buma 2015) and are likely to cause greater stem breakage and tree mortality than promoting recruitment and growth (Oliver 1980;

Dittus 1985; Ibanez et al. 2019). This emphasizes the need to focus on the dynamics of CWD that may occur due to stem breakage and tree mortality, when investigating the impact of frequent TCs on FCS.

Ungulates are an important component of many forest ecosystems worldwide, and they affect the FCS through herbivory on understory vegetation (Forbes et al. 2019; Landuyt et al. 2019; Deng et al. 2023). Usually, selective browsing by ungulates promotes the growth of remaining vegetation and the recruitment of new vegetation, contributing to maintaining the original stand structure (Jones et al. 1994; Wilby et al. 2001). Therefore, the herbivory of ungulates is rarely considered a disturbance in the FCS studies (Forbes et al. 2019). In contrast, excessive and prolonged vegetation consumption (hereafter referred to as overbrowsing) is considered PRD because it reduces the biomass of understory vegetation and alters species composition across landscapes (Hernández and Silva-Pando 1996; Guerisoli and Pereira 2020). Recently, changes in human activity, such as the introduction of alien ungulates and the reduction of hunting pressure, resulted in an increased ungulate population in the Northern Hemisphere (Côté et al. 2004; Takatsuki 2009; Tape et al. 2016). Overpopulation of ungulates has been a wider area of North America (Tape et al. 2016), Europe (Côté et al. 2004; Putman et al. 2011; Hewitt 2011), and Asia (Takatsuki 2009). In these areas, overbrowsing promotes the loss of vegetation, especially for palatable species (Côté et al. 2004). Hindered recruitment of palatable tree saplings has promoted expanding sparseness in gap areas (Shinoda and Akasaka, 2020; Tsujino and Matsui, 2022) and increasing the population of unpalatable species (Tremblay et al. 2006; Enoki et al. 2017; Forbes et al. 2019). Consequently, overbrowsing leads heterogeneous stand structural alterations within landscape. Further, overbrowsing-induced loss of understory vegetation accelerates soil erosion in montane slopes (Mekuria et al. 2007; Labrière et al. 2015; Katayama et al. 2023). For example, a 33-fold increase in sediment production rate has been reported in a Japanese granite area when the understory coverage rate decreased from >60% to <30% (Mizuno et al. 2021). Flores et al. (2020) reviewed the literature on forest ecosystems and hypothesized that soil erosion hinders the re-growth of overstory trees after forest fires in central Amazonia. While the need for management of overbrowsing has been raised (e.g., Guerisoli and Pereira 2020), there is little empirical evidence of the impact on FCS (e.g., Forbes et al. 2019). This knowledge gap hinders the consideration of specific management measures. Especially, the information about the effects of overbrowsing-triggered stand structural alterations and soil erosion on FCS is required for forests on mountain slopes.

1.5. Structure of the dissertation and study sites

1.5.1. Structure of the dissertation

Figure 1-3 displays the structure of this dissertation. This dissertation is based on observational studies in two Japanese forests, each targeting frequent TCs as MPLD or prolonged overbrowsing as PRD. The overarching aim of the dissertation is to quantify the extent and spatial variability of FCS degradation against frequent TCs or prolonged overbrowsing at the stand-scale, and to understand the underlying processes from the perspective of vegetation demography. The dissertation consists of six chapters, including this one. Chapters 2 and 3 address frequent TCs in a subtropical forest in the northern part of Okinawa Island (Fig. 1-3). Chapter 2 examines CWD production at the stand-scale, along with the spatial variability of CWD production. Chapter 3 reports the C stock and associated HR in the DOM at the stand-scale and discusses the role of CWD in the total C stocks and NEP in this forest. Chapters 4 and 5 address overbrowsing and subsequent soil erosion in the southern part of Kyushu Island (Fig. 1-3). Chapter 4 explores the impacts of sporadic soil erosion due to overbrowsing on mature tree growth. Chapter 5 comprehensively quantifies how multiple stand alterations due to overbrowsing affect total C stocks and NECB. Chapter 6 provides a general discussion, summarizing the results of chapters 2–5. It integrates the findings and their implications in the context of disturbance-FCS relationships.

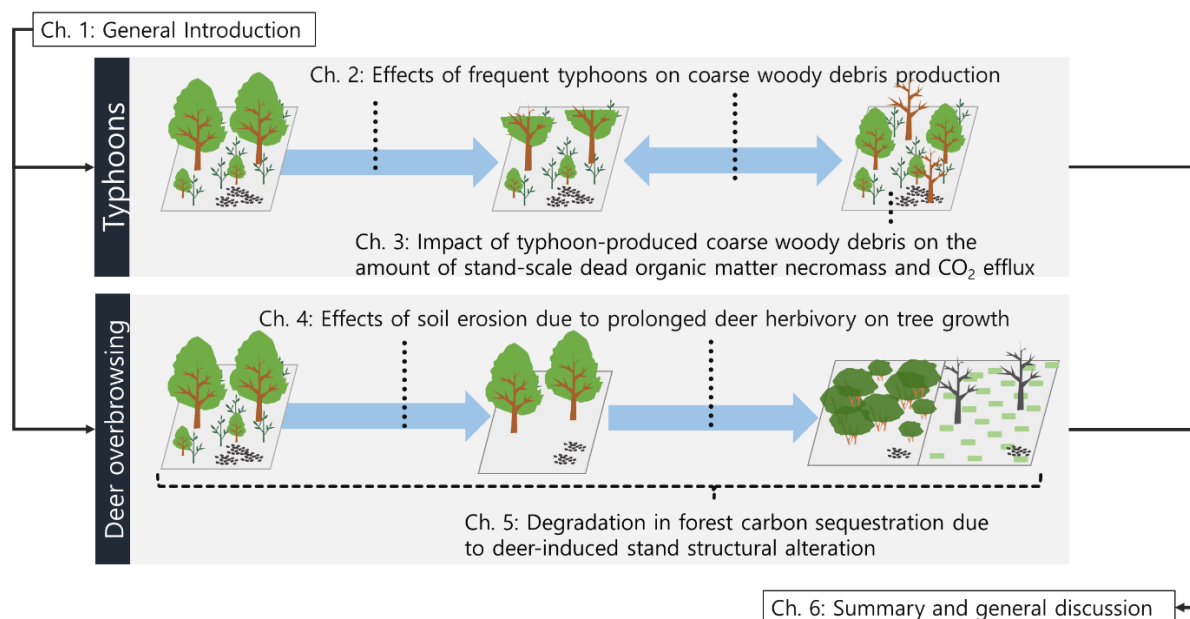


Fig. 1-3. Graphical structure of the dissertation.

1.5.2. Study sites

Studies in chapters 2 and 3 were conducted in a Yona Field (YF), owned by the University of the Ryukyus, in the northern part of Okinawa Island (26°45'N, 128°12'E, 190–210 m a.s.l.). YF is located in a maritime subtropical climate. The annual mean temperature and precipitation from 1976 to 2019 were 20.7 °C and 2505.5 mm, respectively, observed at the nearest weather station (AMeDAS, Japan Meteorological Agency, Oku), 11 km away from the YF. The forest type is a subtropical evergreen broadleaved forest consisting of *Castanopsis sieboldii*, *Schima wallichii*, *Ilex liukiuensis*, *Elaeocarpus japonicus*, and *Symplocos prunifolia* (Matsumoto et al. 2023). In this area, strong winds often occur via typhoons (Amano et al. 1999). For example, 47 typhoons approached YF between 2010 and 2019 (see details in chapter 2). These typhoons resulted in a high amount of leaf litter and FWD supply (Xu 1998; Alhamd and Hagihara 2004) and high tree mortality (Kubota et al. 2004). In YF, the Silviculture Laboratory at the University of the Ryukyus conducted tree level inventory census in a plot with areas of 2500 m², including individual tree height measurements. This comprehensive data sets are ideally suited for monitoring CWD production resulting from stem breakage and standing mortality. Based on above, this study site is targeted for the dissertation.

Studies in chapters 4 and 5 were conducted in a Kyushu University Shiiba Research Forest (SRF), located on southern Kyushu Island (32.37274 °N; 131.14417 °E; 1031–1428 m above sea level). The mean annual temperature and precipitation in the study area were 10.8 °C and 3207.9 mm, respectively (DEIMS-SDR, 2021). The forest type is a mixed forest consisting of deciduous broad-leaved trees, such as *Fagus crenata*, *Quercus crispula*, and *Stewartia monadelphica* as well as evergreen conifers, such as *Abies firma*, *Tsuga sieboldii*, and *Pinus densiflora* (Enoki et al., 2013). Overbrowsing by sika deer (*Cervus nippon*)—a native ungulate in Japan—has occurred in this area since the 1980s (Saruki et al. 2004). Before the overpopulation of sika deer, the study area was entirely covered by understory vegetation, dominated by dwarf bamboo (*Sasamorphia borealis*). Following the overbrowsing, understory vegetation cover has decreased and lost across most of the study area (Saruki et al., 2004). Further, overbrowsing promoted the expansion of unpalatable shrub species, Asebi (*Pieris japonica*) (Tokumoto and Katayama 2024), as well as the expansion of canopy gap areas due to the failure of palatable tree regeneration following overstory mortality (Shinoda and Akasaka 2020). In addition, loss of understory vegetation has been reported to increase soil erosion (Katayama et al. 2023). Given that these documented records are essential for conducting the

survey for the dissertation and are almost impossible to obtain in many other regions, SRF was selected as an optimal study site for the dissertation.

1.6. Supplemental sections: the scope of natural disturbances covered by this dissertation

S.1.1. Expansion of the definition of natural disturbances

In this dissertation, natural disturbances was defined as “Series of events that disrupt ecosystem structure and related environmental conditions, affecting forest carbon sequestration”. Traditional definitions of natural disturbances (e.g. White and Pickett 1985) emphasized that it is a temporally bounded event that abruptly reshapes an ecosystem. This dissertation extends such traditional definitions to include not only single events, but also set of multiple events and continuous events. Thus, natural disturbances in this dissertation includes single pulse- (SPLD), multiple pulse- (MPLD), and press- (PRD) disturbances. By incorporating these disturbances, this dissertation tries to provide a comprehensive framework that covers full aspects of temporal disturbance relation to the forest carbon sequestration (FCS). This perspective is practical because forest ecosystems experience not only isolated events but also ongoing stresses and repeated perturbations, all of which can degrade FCS in various ways (Kurz et al. 2008; Hicke et al. 2012; Pan et al. 2024).

S.1.2. Brief explanation of disturbance types

SPLD refers to a discrete, short-term event that abruptly disrupts an ecosystem, such as single fire, wind-gust, and insect out-break (e.g. White and Pickett 1985). SPLD also stimulate vegetation re-growth through creating opening gaps and resource pulses (Johnstone et al. 2016). Thus, SPLD generally allows the system to retain the resilient vegetation reorganization process (Holling 1973; Gunderson 2000; Johnstone et al. 2016; McDowell et al. 2020). MPLD refers to a series of discrete disturbance events that occur repeatedly within the same system over time, such as repeated fires (Johnstone et al. 2016; Inamine et al. 2022). Although each event is a pulse, but the frequent nature of MPLD means the ecosystem is impacted again before full vegetation recovery is achieved (Oliver 1980; Sturtevant and Fortin 2021). Hence, MPLD potentially shapes the system a oscillate state between disturbed and recovered state without

ever fully stabilized state (Oliver 1980; Ratajczak et al. 2017; Inamine et al. 2022). PRD refers to a long-term, persistent disturbance that continues without significant respite, such as prolonged droughts and ungulate overbrowsing (Bender et al. 1984). Due to its ongoing nature, PRD does not allow the system to recover during the disturbance (Bender et al. 1984; Ratajczak et al. 2017). This means PRD gradually force ecosystems toward alternative states, as species that cannot tolerate the prolonged impact are eliminated and replaced by those better adapted to the altered conditions (Wootton and Stouffer 2016; Santillan et al. 2020; Leroux et al. 2020; Inamine et al. 2022).

S.1.3. Spatio-temporal scale dependency of disturbance classification

One of the important issue by classifying SPLD, MPLD, and PRD is context dependency of measurement time frame. For example, a three-year drought would be considered a PRD when assessing the response of a forest ecosystem within 10 years, but it could be considered a SPLD when assessing the response over 1000 years. Thus, the temporal classification of natural disturbance is essentially subjective. However, vegetation turnover and recovery times serve as useful baselines to conduct a more objective classification (Holling 1973; Batllori et al. 2020; Seidl and Turner 2022). Based on these baseline, SPLD can be recognized as a disturbance that occurs at intervals longer than vegetation turnover or recovery time (Holling 1973; Jentsch and White 2019). MPLD can be recognized as disturbances occurring shorter durations than the vegetation recovery time (Oliver 1980). PRD can be recognized as a disturbance that do not allow vegetation recovery, and continuing for a period exceeding the turnover time (Bender et al. 1984; Leroux et al. 2020). These classification baselines are dependent on the ecosystem, but vegetation turnover and recovery time can be evaluated through objective observation such as tree inventory survey.

Spatial scale also affects disturbance classification. Increasing the observation scale can transform localized, short-term disturbances into broader, continuous patterns (Levin 1992; Ratajczak et al. 2017). For example, a wind-gust may cause SPLD impacts at stand scale, but when observed at a landscape scale, scattered tree mortality may create a mild, ongoing disturbance pattern like PRD (Zeng et al. 2009). The spatial characteristics of each disturbance can be explained in a unified way in view of the vegetation recovery after the disturbance. SPLD tends to affect different areas and different times within landscape. Thus, SPLD often shapes a mosaic pattern in landscapes, where patches of different vegetation recovery stages

coexist (Turner and Gardner 2015). This mosaic pattern is recognized as “patch dynamics” theory in ecology (White and Pickett 1985; Luisa 2012; Jentsch and White 2019). Similar to SPLD, MPLD also occurs heterogeneous within the landscape, whereas PRD may produce a large number of patches that are biased towards the immediate aftermath of the disturbance or the early stages of vegetation recovery (Oliver 1980; Johnstone et al. 2016). For this reason, the pattern of mosaic created by MPLD may differ from that created by SPLD. PRD has expanding spatial impact, often gradually homogenizing landscapes by imposing persistent impact across wider areas (Ratajczak et al. 2017).

The “disturbance continuum” concept (Łaska 2001) suggests a positive relationship between disturbance frequency and spatial scale for SPLD. However, this does not apply to MPLD and PRD, as cumulative effects and recovery limitations must be considered.

Although SPLD, MPLD and PRD are originally located in continuous spectrum of space and time, the degree of their influence on stand structure and FCS can be observed as discrete, different stages. For example, consider the case where the frequency of MPLD increases. Whether or not such MPLD can be considered a PRD depends on the pattern of vegetation recovery. If species that can recover rapidly, such as highly sprouting species, are preferentially selected to survive, and those that cannot are selectively eliminated, highly frequent MPLD has the potential to reorganize vegetation into an alternative state than before—thus this can be identified as PRD in observations of vegetation structure. Overall, the classification of disturbances is practically useful for evidence-based FCS management.

S.1.4. Differences between press disturbance and stress

In ecological research, stress is recognized as a chronic environmental constraint that affects organismal performance by limiting productivity, survival, or reproduction (Lichtenthaler 1996). Stress often resembles PRD because of prolonged nature. Stress primarily operates at the individual level (Levitt et al. 1972; Lichtenthaler 1996; Kranner et al. 2010). If the stress has a wide-ranging and long-lasting impact on the ecosystem, it is considered to be a PRD. For example, a severe multi-year drought may initially cause water stress in trees, but if it persists, widespread tree mortality can lead to irreversible shifts in community composition (i.e., it can be recognized as PRD). On the contrast, water deficient in polar and desert ecosystems are not recognized as PRD because the ecosystem is stable despite the presence of stress (Lathrop and Rowlands 1983).

Chapter 2: Effects of frequent typhoons on coarse woody debris production

2.1. Introduction

Wind gusts are a common phenomenon in coastal areas of temperate and tropical zones (Mitchell 2013; Ibanez et al. 2019). A wind gust generally causes sea salt deposition, stem breakage, crown defoliation and subsequent mortality, and uprooting (Ackerman et al. 1991; Everham and Brokaw 1996; Choi et al. 2014). This means a wind gust produces dead wood from living trees as coarse woody debris (CWD). Especially, tropical cyclones (TC)—including hurricanes and typhoons— quickly convert large amounts of living biomass into CWD (Harmon et al. 1986; Wu et al. 2019). These produced CWD will be decomposed and release stored carbon (C), thereby increasing heterotrophic respiration (HR) from the ecosystem. Therefore, understanding CWD production processes resulting from TC is crucial for assessing the forest C sequestration (FCS) in forests, especially around the maritime zones.

Previous studies about relationships between TC and FCS have primarily focused on episodes of forest damage and vegetation recovery following a single TC (Schaetzl et al. 1989; Lugo and Waide 1993; Everham and Brokaw 1996; Cooper-Ellis et al. 1999; Lugo 2008; Šamonil et al. 2010). These studies have demonstrated that a single TC produced CWD across the stand or landscape (e.g., Everham and Brokaw, 1996). In areas where large amounts of CWD are produced, are often become open-canopy conditions (Fernandez and Fetcher 1991; Lin et al. 2003; Turton and Alamgir 2015), while vegetation in these areas rapidly recovered through the regrowth of broken individuals, resprouting from damaged trees, and growth release of residual trees due to reduced competition (Everham and Brokaw 1996; Bellingham et al. 1996; Lin et al. 2011). In contrast, the impacts of frequent TCs have not been well documented (Bonilla-Moheno 2010). Everham and Brokaw (1996) posed two hypotheses regarding the impact of frequent TCs: (I) if frequent TCs selectively remove specific trees, then only portion of biomass will be converted to CWD (i.e., CWD production is limited by a certain threshold characterized by the stand); or (II) if frequent TCs remove all trees, then all part of biomass will be converted to CWD (i.e., CWD production is not limited by the stand characteristics). Although the frequency of TC is expected to increase with climate change (Kossin et al. 2020; Klotzbach et al. 2022), these hypotheses remain untested due to a lack of

observational studies (Bonilla-Moheno 2010; Buma 2015; Lo et al. 2020). To improve our understanding, it is crucial to examine CWD production patterns in forests that already experience frequent TCs.

In addition to the uprooting mortality, frequent TCs causes stem breakage due to physical shocks from the wind and collisions between tree crowns (Chiba 2000; Onoda and Bando 2021). Physical damage to tree crowns and stems can lead to standing tree death (Dittus 1985; Lugo and Waide 1993; Walker 1995; Sato et al. 2017). These indicate that frequent TCs generate both standing CWD (CWD_{snag}) and fallen CWD (CWD_{log}) (Yoda and Kira 1982; Harmon et al. 1986). Generally, CWD production against TCs is often calculated based on the assessment of tree mortality from the detection of dead trees by aerial photography and/or on-site census immediately after the TC (Arriaga 2000; Chambers et al. 2007; Chao et al. 2009; Sato et al. 2017; Šamonil et al. 2017; Forzieri et al. 2020). However, most of these approaches do not consider the CWD production due to stem breakage and lagged-subsequent standing death (Ulanova 2000; Mitchell 2013). To detect these, it is effective to track changes in tree height and mode of death using individual tree inventory surveys. In addition, both CWD_{snag} and CWD_{log} production may vary with biotic and abiotic factors, such as tree species (Foster et al. 1998; Xi et al. 2008), tree size (Foster et al. 1998; Canham et al. 2001), and topography (Huggard et al. 1999; Ulanova 2000). This suggests the need to consider the spatial heterogeneity of CWD_{snag} and CWD_{log} production at individual tree levels when investigating forests where frequent TCs occur.

The northern part of Okinawa Island in Japan features subtropical forests in a maritime subtropical climate. On this island, frequent TCs often approached (Amano et al. 1999). These TCs have been reported to cause sea salt deposition (Sakihama and Tokuyama 2005; Sakihama et al. 2008), defoliation (Xu 1998), and stem breakage (Enoki et al. 2014; Takashima et al. 2021). In addition, high tree mortality has been reported (Kubota 2003; Kubota et al. 2004). However, it has not been evaluated that the impact of frequent TCs on productions and the patterns of CWD_{snag} and CWD_{log} in this area. This chapter aimed to understand the characteristics of CWD_{log} and CWD_{snag} productions in this forest, which suffered from frequent TCs. For this aim, inventory survey data was analyzed to evaluate the temporal dynamics of stand structure and CWD production, as well as the influence of tree species and size, topography, and stand structure on the production of CWD_{log} and CWD_{snag} .

2.2. Methods

2.2.1. Analyzed data

This study used the tree inventory survey data from the Laboratory of Silviculture, University of the Ryukyus. This data includes species name, diameter at breast height (DBH), and tree height for overstory trees with DBH ≥ 3 cm in a 0.25 ha study site in the Yona Field (YF) at the University of the Ryukyus (Fig. 2-1a). The forest type in this site is a subtropical evergreen broadleaved forest consisting of *Castanopsis sieboldii*, *Schima wallichii*, *Ilex liukiuensis*, *Elaeocarpus japonicus*, and *Symplocos prunifolia* (Matsumoto et al. 2023). In this site, tree status (alive or dead), mode of death (standing death or fallen death), species name, DBH, and tree height were recorded in 2013, 2016, and 2019 using steel tape (PKM-20, TRUSCO, Tokyo, Japan) and extendable rods (FT-12, Myzox Co., Ltd, Aichi, Japan). In addition, these data are recorded in each of 100 subplots with 5 m $\times$ 5 m size (Fig. 2-1b). According to the University records, the study site had been heavily logged until the 1940s and had been disturbed by selective logging until the 1980s. Since then, this site has not been subjected to logging or other human activity (Hirata 1979). As shown in chapter 1, the annual mean temperature and precipitation in the study site were 20.7 °C and 2505.5 mm, respectively. According to the records of the nearest weather station (AMeDAS, Japan Meteorological Agency, Oku), 11 km away from the study site (Fig. 2-1a), the number of days per year when the maximum hourly wind speed exceeds 10 m s⁻¹ is 16.2 ± 6.2 days (Fig. 2-1d). According to the TCs database (<http://agora.ex.nii.ac.jp/digital-typhoon/>), there were 47 TCs (4.7 ± 2 TCs yr⁻¹) that approached the study site between 2010 and 2019, with the center of each TC passing within 300 km of the study site (Table S2-1). Note that this study did not identify the spatial size or strength of each TC. Normally, it is difficult to observe such properties accurately, and it is also not possible to simply correlate them with the degree of damage to the ecosystem (Peters et al. 2011). Therefore, this chapter focuses only on the frequency of typhoons and wind gusts.

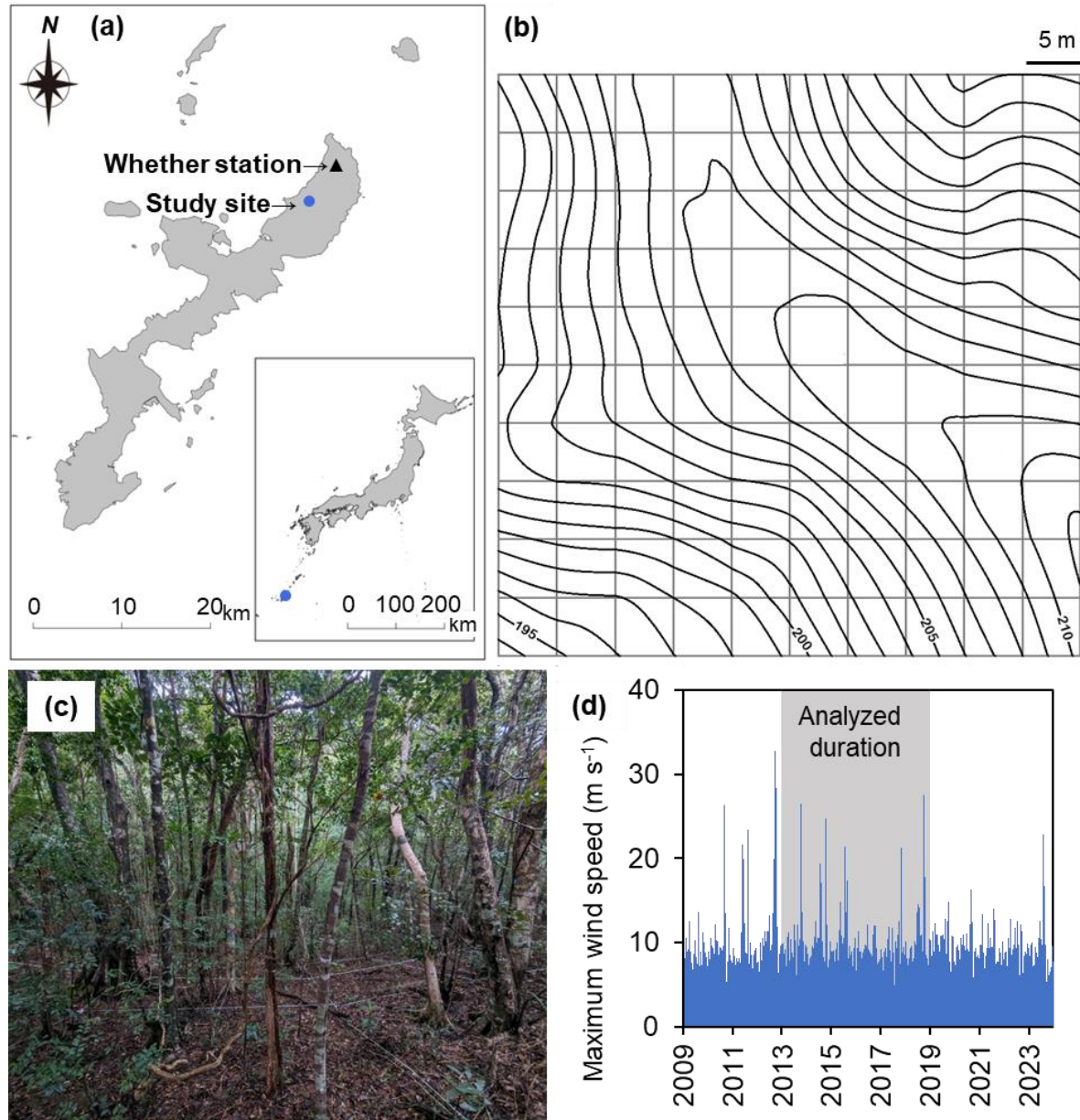


Fig. 2-1. Location of the study site (blue circle) and near whether station (black triangle) in Okinawa Island, Japan (a), map of the study site (b), photograph of the study site (c), and daily maximum wind speed in the weather station (d). In panel b, the Grid of the study site indicates subplots (5 m × 5 m), and contour intervals are 1 m.

2.2.2. Estimation of coarse woody debris production

CWD production ($\text{g C m}^{-2} \text{ yr}^{-1}$) was calculated based on the dataset. The production of CWD_{snag} was defined as the amount of new-standing deadwood biomass produced during the inventory survey period. The production of CWD_{log} was defined as the amount of new fallen individuals produced during the inventory survey period and the amount of new broken stems

(see Eq. 2-4). In the inventory survey, stem biomass (g m^{-2}) for each tree of *C. sieboldii* and *S. wallichii* was estimated by the species-specific allometric equation as follows (Nakasuga et al. 2019):

$$\log_{10} W = 0.9864 \log_{10} D^2 H - 1.6035 \quad (\text{Eq. 2-1}),$$

$$\log_{10} W = 0.6559 \log_{10} D^2 H - 0.4153 \quad (\text{Eq. 2-2}),$$

where W is individual-level stem biomass (kg), D is DBH (cm), and H is tree height (m). Equations 2-1 and 2-2 are the equations for *C. sieboldii* and *S. wallichii*, respectively. The stem biomass for each tree, except for *C. sieboldii* and *S. wallichii*, was estimated by general allometric equations for Japanese tree species as follows (Ishihara et al. 2015):

$$\ln(W) = -2.589 + 1.1915 \ln(D) + 0.728 \ln(H) + 0.603 \ln(\rho) \quad (\text{Eq. 2-3}),$$

where ρ is species-specific wood gravity (g m^{-3}). The ρ -values were collected from literature values reported from Okinawa Island (Okinawa Prefectural Forest Resources Research Center 2022) (Table S2-2). Genus-level and family-level average values were used when literature values were not available. In this study, the stand-scale biomass in 2013 was calculated as the sum of the individual biomass of living trees. The stand-scale biomass was converted to C stocks, assuming the stem C concentration of 0.480 g C g^{-1} (Martin et al. 2018).

The stand-scale biomass in 2016 and 2019 was calculated using the sum of biomass increase from tree growth and the biomass loss from CWD production:

$$S_{t+3} = S_t + G - P_s - P_{l_f} - P_{l_b} \quad (\text{Eq. 2-4}),$$

where S is stand-scale stem biomass at year of t and $t + 3$, G is stem biomass growth of living trees, P_s is CWD_{snag} production, and both P_{l_f} and P_{l_b} are CWD_{log} production (Fig. 2-2). P_s and P_{l_f} indicate the total amounts of standing death and fallen death, respectively. P_{l_b} indicates the mass of broken stems (see Eq. 2-7) (Fig. 2-2). G is calculated based on the difference in individual living tree biomass between the two measurement periods as follows:

$$G = \sum (W_{k,t+3} - W_{k,t}) \quad (\text{Eq. 2-5}),$$

where W_k is the stem biomass of tree k . During the measurement period, some trees decrease their height due to stem breakage. These individuals' biomass and the amount of CWD_{log} production due to stem breakage (i.e., P_{l_b}) were calculated as follows. To begin, we set three assumptions: (1) the tree shape is a cone, (2) the biomass and the volume of the tree are directly proportional to each other, and (3) the tree height before the breakage is equal to the height measured in the prior period. Based on these assumptions, tree biomass of individuals with stem breakage and P_{l_s} were calculated using the similarity of cone volume:

$$W_b = W_i - W_{l_b} \quad (\text{Eq. 2-6}),$$

$$P_{l_b} = W_i \frac{\left(\sqrt{H_t^2 + 0.5D_{t+3}^2} - \sqrt{H_{t+3}^2 + \left(H_{t+3} \frac{0.5D_{t+3}}{H_t} \right)^2} \right)^3}{\left(\sqrt{H_t^2 + 0.5D_{t+3}^2} \right)^3} \quad (\text{Eq. 2-7}),$$

where W_b is the individual biomass with stem breakage, and W_i is the ideal biomass of individual trees, assuming no stem breakage occurs. W_i was calculated from Eqs. 2-1, 2-2, or 2-3 using tree height measured in the prior period.

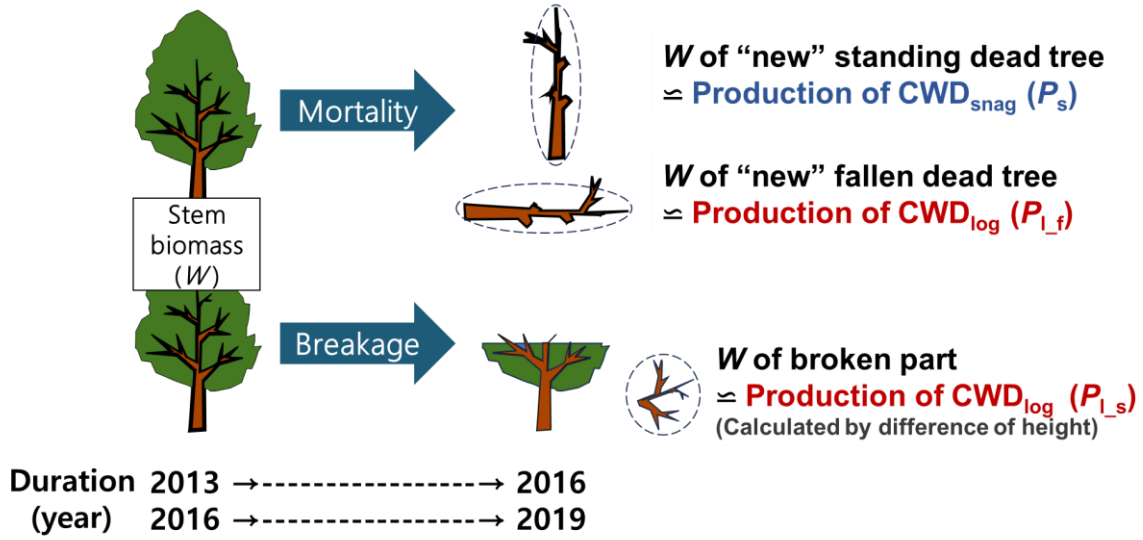


Fig. 2-2. Diagram of coarse woody debris (CWD) production calculation. The terms P_s , P_{l_f} , and P_{l_s} are described in Eq. 2-4.

2.2.3. Evaluation of characteristics of coarse woody debris production

As the location data for individual trees was unavailable, the magnitude of spatial variability in CWD production was evaluated based on the coefficient of variation (CV) of CWD production among subplots instead (Fig. 2-1b). This evaluation was done by dividing the measurement durations (2013–2016 and 2016–2019) as well as CWD types (CWD_{log} and CWD_{snag}). To evaluate the spatial distribution patterns of CWD production, semivariogram analysis was employed as follows (Gora et al. 2019):

$$\gamma(h) = \frac{\sum \{z(x_i) - z(x_{i+h})\}^2}{2N(h)}$$

(Eq. 2-8),

where $\gamma(h)$ is the semivariance between subplots separated by the distance interval h , $N(h)$ is the number of pairs in the distance interval h , and z is the objective value at subplot x_i and x_{i+h} . Using subplot distances, we calculated γ values for distances up to 50 m in 5 m increments. To address frequent zero values in subplot-level CWD production, CWD production values were $\log(x + 1)$ -transformed before analysis (Gora et al., 2019). Semivariograms were approximated with four models: Linear, Exponential, Spherical, and Gaussian. The best model was chosen based on the lowest residual sum of squares (RSS) from regression analysis. Post-selection, we identified specific parameters of the chosen model, namely the nugget, sill, and range. The nugget, sill, and range represent $\gamma(0)$, $\gamma(h)$ without the effects of autocorrelation, and length of autocorrelation, respectively. Semivariogram analysis was performed using GS+ for Windows ver. 10 (Gamma Design, Plainwell, MI, USA).

The effects of tree characteristics, topography, and stand density on the probability of CWD production were evaluated using a generalized linear mixed model (GLMM) to explore the factors driving spatial variability of CWD production. In this analysis, the objective variable was a binary value that indicated whether individual trees produced CWD (1) or not (0). These binary values were generated for each measurement duration and CWD type. Tree character variables included species-specific wood gravity, DBH, tree height, and slenderness ratio (i.e., $\text{DBH} / \text{Height} * 100$; %). Topographic variables included elevation (m), curvature (positive value shows convex, and vice versa), slope angle ($^\circ$), and slope aspect (southwest slope, ridge, and northeast slope) at the subplot where each tree is located. Three types of slope aspects were converted to two binary classes by on-hot encoding, i.e., northeast slope (1) or not (0) and southwest slope (1) or not (0). Stand density variables included stem density (stems ha^{-1}), stem basal area ($\text{m}^{-2} \text{ ha}^{-1}$), and stem packing index (SPI) at the subplot where each tree is located. SPI was calculated as follows:

$$I = B \frac{1 - S}{S_a}$$

(Eq. 2-9),

where I is the stem packing index, B is the basal area of the subplot, S is the stem density of the subplot, and S_a is the overall average of stem density from the 100 subplot. The absolute value of SPI indicates the extent of basal area, and a positive sign indicates that basal area was achieved by a relatively higher number of small stems, while a negative sign indicates that basal area was achieved by a smaller number of large stems. Stand density variables were taken from

the year before the CWD production period. For example, stand density variables calculated in 2013 were used for CWD production from 2013–2016. Given that tree characteristic variables, topographic variables, and stand density variables interact with each other (Fig. S2-1), there was a high possibility that statistics confounding when evaluating the relationship between individual explanatory variables and the dependent variable (Pourhoseingholi et al. 2012). To avoid this concern, a multiple regression model was created that included all explanatory variables (Pourhoseingholi et al. 2012). In addition, since these explanatory variables have different units and a range of values, these were standardized to have a mean of 0 and a standard deviation of 1 before model development. The model accounted for two durations of CWD production (i.e., 2013–2016 and 2016–2019), treating these durations as a random effect. This modeling was performed using R software version 4.3.2 for win.x86 with packages “lme4” (Bates 2016) and “modelsummary” (Arel-Bundock 2022).

2.3. Results

2.3.1. Dynamics of stand structure

The stem density at the study site in 2013, 2016, and 2019 were estimated to be 5756, 6020, and 6408 stems ha^{-1} (Fig. 2-3). Similarly, total stem biomass at the study site in 2013, 2016, and 2019 were estimated to be 7067.3, 7069.8, and 7184.7 g C m^{-2} (Fig. 2-4). From 2013–2016, 558 trees (38.8% of trees in 2013) decreased their height due to stem breakage. Similarly, 554 trees (36.8% of trees in 2016) decreased their height from 2016–2019. The mortality rate from 2013–2016 was 3.8% (standing death; 48 trees, fallen death; 6 trees), and from 2016–2019 was 4.1% (standing death; 53 trees, fallen death; 8 trees). From 2016–2019, trees with stem breakage had a mortality rate of 5.2% higher than those without breakage (3.4%).

In the study site, 38 tree species were recorded. Among them, *C. sieboldii* had the highest stem density, followed by *Myrsine sequinii*, *Ilex liukuensis*, *Syzygium buxifolium*, and *Elaeocarpus japonicus* (Fig. 2-3a). Although *C. sieboldii* dominated in the stand, its stem density consistently decreased from 2013 to 2019; the contribution to stem density decreased from 19% in 2013 to 15% in 2019. Stem density was highest in trees with DBH of <15 cm, and these populations showed an increasing trend by year (Fig. 2-3b). Regarding tree height, there were highest populations in height of 5–7 m, and the number of individuals with height <7 m

showed an increasing trend (Fig. 2-3c). In contrast, the number of individuals with height >7 m showed a decreasing trend. Similarly, the number of individuals with a slenderness ratio of <125 showed an increasing trend, whereas those with a slenderness ratio >125 showed a decreasing trend (Fig. 2-3d).

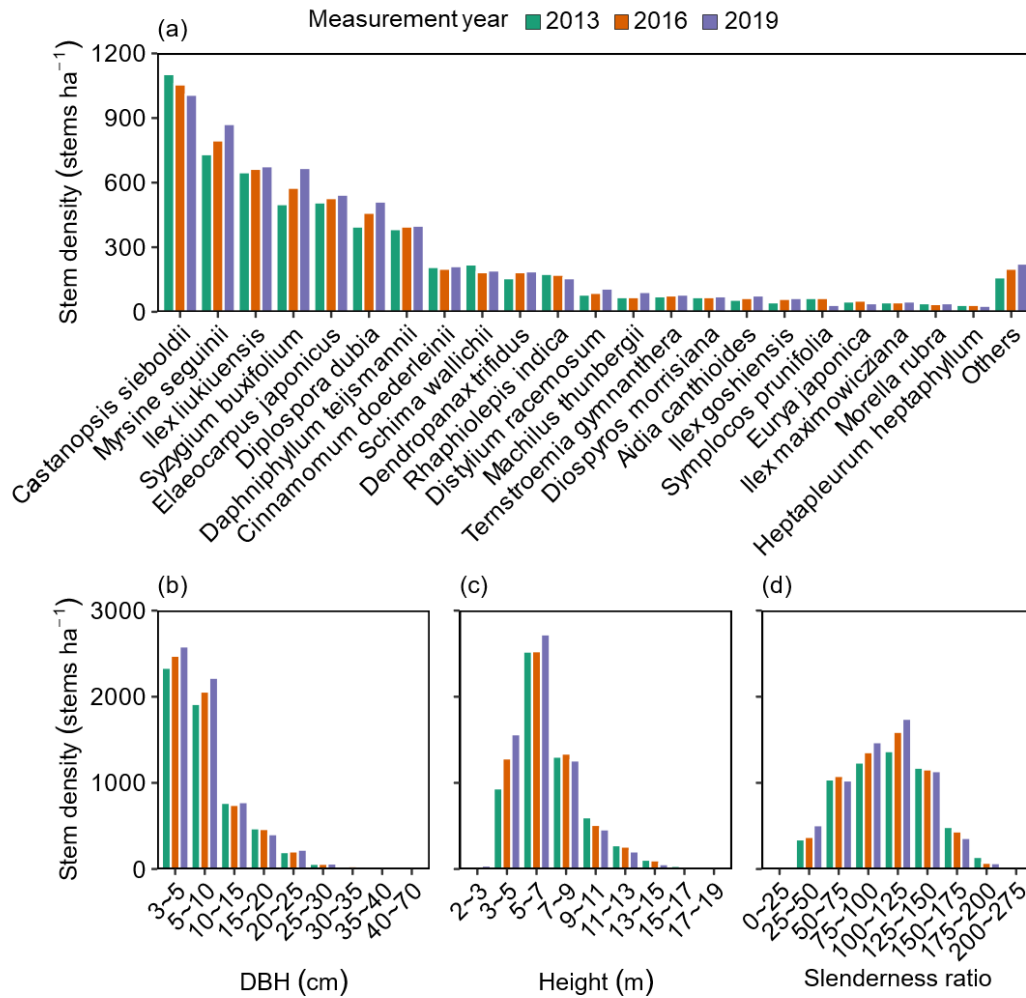


Fig. 2-3. Differences in stem density by species (a), diameter at breast height (DBH) (b), tree height (c), and slenderness ratio (d) in 2013, 2016, and 2019.

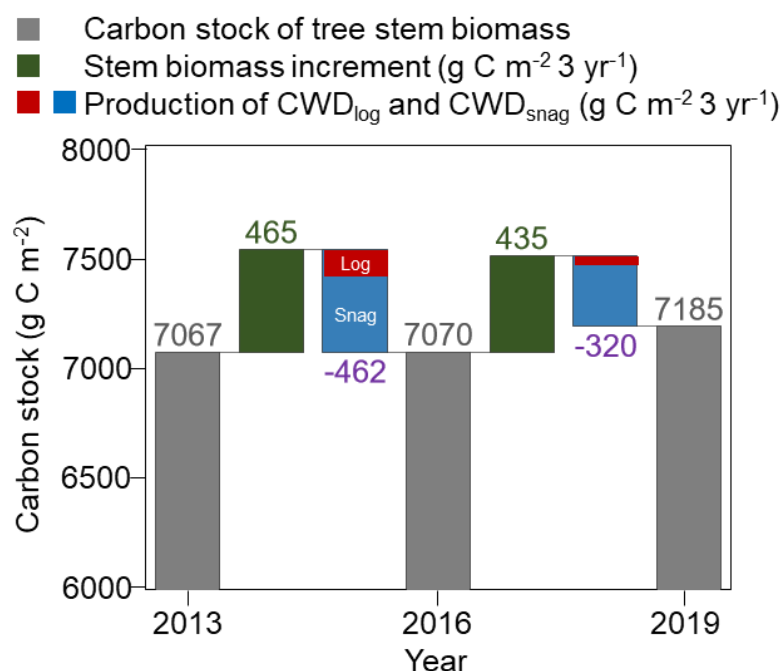


Fig. 2-4. Water flow diagram of the changes in stand scale stem biomass driven by stem biomass increment and CWD production.

2.3.2. Amount of coarse woody debris production

Production of CWD was estimated to be 462.4 g C m⁻² (154.1 g C m⁻² yr⁻¹) from 2013–2016, and 319.7 g C m⁻² (106.6 g C m⁻² yr⁻¹) from 2016–2019 (Fig. 2-4). The variation in CWD production across the two durations was attributed to the difference in the production of CWD_{log}. The production of CWD_{log} from 2013–2016 (44.6 g C m⁻² yr⁻¹) was 4-fold higher than that from 2016–2019 (12.2 g C m⁻² yr⁻¹). In contrast, the production of CWD_{snag} was similar in both periods (109.5 g C m⁻² yr⁻¹ from 2013–2016; 94.3 g C m⁻² yr⁻¹ from 2016–2019), accounting for >70% of total CWD production. The total production of CWD_{snag} and CWD_{log} was closely equivalent to the amount of tree stem growth (155.0 g C m⁻² yr⁻¹ from 2013 to 2016 and 144.9 g C m⁻² yr⁻¹ from 2016 to 2019). Consequently, there was minimal change in the stem biomass from both 2013–2016 and 2016–2019.

2.3.3. Spatial variation pattern and controlling factor of coarse woody debris production

High spatial variation was found for CWD production at the subplot level. The CVs of CWD production varied 210.2–878.5% for CWD_{log} and 207.8–252.8% for CWD_{snag}. According

to the result of semivariogram analysis, there was no spatial dependence of CWD production (Table 2-1). Spherical and exponential models were chosen for the semivariogram models of CWD_{log} and CWD_{snag} production. However, the range of these models was <7 m, which is shorter than the length of the subplot (i.e., side length is 5 m, diagonal length is about 7.1 m).

There was a relationship between the occurrence probability of CWD production and the characteristics of individual trees (Table 2-2). The occurrence probability of CWD_{log} was higher for individuals with lower wood gravity, higher tree height, higher slenderness ratio, and higher elevation (Fig. 2-5). A higher probability of CWD_{snag} production was found for individuals with lower wood gravity, higher tree height, lower DBH, and lower slenderness ratio (Fig. 2-5). Especially, the probability of CWD_{log} production reached the highest possibility ($\cong 1$) when the standardized tree height >2 (i.e., average + 2*SD) (Fig. 2-5c).

Table 2-1. The result of semivariogram models for log (x + 1)-transformed production of coarse woody debris (CWD) from 2013 to 2016 and 2016 to 2019.

	CWD _{log}		CWD _{snag}	
	2013–2016	2016–2019	2013–2016	2016–2019
Model	Spherical	Exponential	Exponential	Exponential
Range (m)	7.01	2.53	2.87	3.56
Nugget	0.00010	0.049	0.0010	0.11
Sill	0.29	0.41	1.08	1.18
R^2	0.058	0.57	0.25	0.77

Abbreviations: CWD_{log}, downed coarse woody debris; CWD_{snag}, standing coarse woody debris; R^2 , coefficient of determination.

Table 2-2. The results of modeling probability of CWD production. R^2 is the overall model's marginal R^2 . The results with $p < 0.05$ are shown in bold face.

	CWD _{log} ($R^2 = 0.14$)		CWD _{snag} ($R^2 = 0.31$)	
	Estimate	p	Estimate	p
Tree characteristics				
Wood gravity	-0.23	<0.001	-1.0	<0.001
DBH	-0.20	0.0690	-0.60	0.031
Tree height	0.88	<0.001	0.52	0.007
Slenderness ratio	0.24	<0.001	-0.41	0.044
Topography				
Elevation	0.32	<0.001	0.24	0.185
Slope angle	-0.036	0.491	-0.26	0.056
Curvature	-0.088	0.081	-0.22	0.093
Slope aspect				
Northeast slope or not	0.21	0.185	0.66	0.118
Southwest slope or not	-0.15	0.313	0.15	0.687
Stand structure				
Stem density	0.23	0.103	0.13	0.731
Basal area	-0.022	0.688	0.12	0.418
Stand packing index	0.17	0.182	-0.056	0.861

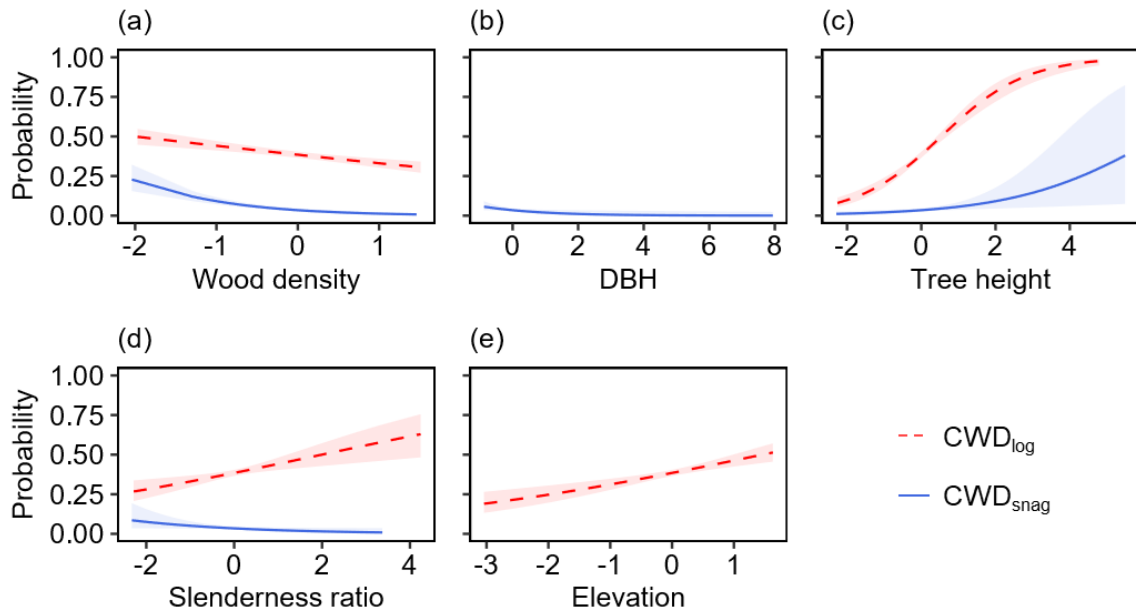


Fig. 2-5. Partial prediction lines of probabilities of CWD_{log} and CWD_{snag} production with $p < 0.05$. The X-axis explained standardized variables. The shaded area indicate the 95% confidence intervals.

2.4. Discussions

2.4.1. Production of coarse woody debris by frequent tropical cyclones

The main finding of the present study was the total production of CWD was nearly equal to the amount of tree growth, restricting stem biomass accumulation in the study site (Fig. 2-4). This ratio of CWD production to tree growth was similar to that of infrequent and catastrophic TC. For example, Hurricane Katrina, hitting the southeastern United States of America in 2005, produced CWD equivalent to 50–140% of the annual net C absorption by U.S. forests (Chambers et al. 2007). A meta-analysis collecting catastrophic TC in Europe from 2000–2018 also reported that catastrophic TC destroys 35–70% of forest area and produces CWD equal to or greater than the annual net C absorption of the remaining forests (Forzieri et al. 2020). Based on the above, if it can be assumed that CWD production in the present study site is mainly due to TC, then the present study implies that frequent TCs, due to its cumulative nature, may generate enough CWD to offset C accumulation by tree growth like episodes of catastrophic TC. This means that the frequent TCs do not convert all of the biomass to CWD at once, but instead continue to generate CWD in parts, supporting hypothesis (I) proposed by Everham and Brokaw (1996). Some evidence found in the present study support that much of the CWD production in this site will be related to TC.

2.4.2. Possible process of coarse woody debris production

The CVs of both CWD_{log} and CWD_{snag} production were $>200\%$, indicating that CWD was produced heterogeneously within the study site. Despite of this, semivariogram analysis did not show any spatial cluster pattern for both CWD_{log} and CWD_{snag} production at the subplot level (Table 2-3). This suggests that clustering patterns may exist at spatial scales larger than the study site (50×50 m), or smaller than the subplots (5×5 m) in the study site. The latter possibility was partially explained by the result of GLMM model as discussed below (Table 2-2).

The higher production of CWD_{log} from 2013–2016 was observed compared to 2016–2019 (Fig. 2-4). Weather records from AMeDAS-Oku during 2013–2016 show that, there were 55 days with daily maximum wind speeds $>10 \text{ m s}^{-1}$, and 6 days $>18 \text{ m s}^{-1}$ which is the threshold for named TCs by the World Meteorological Organization (Typhoon Committee 2015). The

number of such days was fewer in 2016–2019, with 40 days $>10 \text{ m s}^{-1}$ and 2 days $>18 \text{ m s}^{-1}$ (Fig. 2-1d). This pattern supports the relationship between the frequency of TCs and $\text{CWD}_{\log}$ production. In addition, results from GLMM indicated that the probability of $\text{CWD}_{\log}$ production increases for individuals with lower wood gravity, higher tree height, higher slenderness ratio, and higher elevation (Table 2-2). These results were consistent with previous studies discussing the susceptibility of trees to stem breakage against TCs. It has been reported that lower wood gravity (Petty and Swain 1985) and higher slenderness ratio (Huggard et al. 1999; Wonn and O'Hara 2001) increases the vulnerability of stem breakage to physical wind shocks. Furthermore, individuals located at higher elevation or those with higher heights are more exposed to wind than others (Dittus 1985; Reilly 1991; Van Bloem et al. 2005). In particular, the present study found that $\text{CWD}_{\log}$ is more likely to be produced when the standardized height exceeds 2 (Fig. 2-5c), which is approximately equivalent to 10 m in raw value of height. In other words, emergent trees, i.e., trees that exceed the threshold height of 10 m in the present study site, are highly susceptible to stem breakage. This inference is partially supported by the consistent population decline observed in individuals taller than 7–9 m (Fig. 2-3c). Additionally, the number of individuals with a slenderness ratio >125 showed a decreasing trend, whereas those with a slenderness ratio <125 increased (Fig. 2-3d). This suggests that stem breakage reduces tree height, consequently increasing the slenderness ratio. Overall, these findings indicate that, in the study site, $\text{CWD}_{\log}$ is primarily produced when emergent trees and/or individuals with lower physical strength suffer stem breakage due to wind impacts.

In the present study site, CWD_{snag} accounted $>70\%$ of total CWD production (Fig. 2-4). This result is inconsistent with previous studies that TCs produce CWD primarily as $\text{CWD}_{\log}$ (Schaetzl et al. 1989; Everham and Brokaw 1996; Cooper-Ellis et al. 1999; Lugo 2008; Šamonil et al. 2010). Despite of this, it can be posited that TCs play a pivotal role in CWD_{snag} production. Previous studies have demonstrated that TCs leads to tree decline through defoliation and stem breakage, leading subsequent mortality (Dittus 1985; Lugo and Waide 1993; Walker 1995; Sato et al. 2017). Additionally, studies have documented the transportation of sea salt to the present study site due to wind gusts (Sakihama and Tokuyama 2005; Sakihama et al. 2008). Salt stress is known to cause standing tree death (Jimenez et al. 1985; Desantis et al. 2007; Fan et al. 2014). Indeed, trees with stem breakage had a higher mortality rate of 5.2% than that of individuals without breakage (3.4%) during 2016–2019 in the present study site. Subsequent mortality after

stem breakage was supported by higher probability of CWD_{snag} production for individuals with lower wood gravity and higher tree height (Table 2-3). Further, negative relationships between slenderness ratio and probability of CWD_{snag} production implies that mortality of individuals with increased slenderness ratio due to stem breakage (Fig. 2-5d).

Although *C. sieboldii*, the dominant species in the present study site, is known to have a high regeneration rate through sprouting (Enoki 2003), their population has been in reduced (Fig. 2-3a). This suggest that regeneration ability of *C. sieboldii* may be exceeded by the tree mortality caused by TC. Therefore, the present study suggests that the frequent TCs may be promoting CWD_{snag} production by repeated defoliation, stem breakage, and salt deposition. Given that the present study did not show the direct evidence for process of CWD_{snag} production against TCs, future study is required to obtain more detailed causal inference.

From the above, the stand dynamics and the CWD production in the study site is considered as follows (Fig. 2-6). Here, the vulnerable individual are broken stems (i.e., produced CWD_{log}) and/or became standing death (i.e., produced CWD_{snag}) due to the wind gust (Dittus, 1985; Huggard et al., 1999). For example, stem breakage of particularly higher height trees. At the same time, the opening of the canopy creates a light gap, which promotes the growth and sprout renewal of the remaining individuals (Enoki 2003; Abbas et al. 2020). However, in the study site, when the canopy regenerates to a certain threshold, production of CWD_{log} and CWD_{snag} occurs again (Dittus, 1985). As the cumulative effect of wind gusts, standing death of trees might be promoted (Dittus, 1985; Lugo and Waide, 1993). Consequently, at the study site, it can be considered that the accumulation of tree biomass continues to be restricted with continued production of CWD.

The present study emphasizes the importance of measuring tree height when exploring the impacts of frequent TCs on FCS. Although observations of stem breakage and tree mortality have been conducted in this region (Kubota 2003; Enoki 2003; Kubota et al. 2004; Enoki et al. 2014), changes in the height of individual trees have not been tracked. For instance, Biodiversity center of Japan (<https://www.biodic.go.jp/moni1000>) have measured girth of breast height (GBH) at the 1 ha vegetation dynamics observation site (YN-EB1, 126°49'N, 128°5'E) near the present study site since 2004, while has not measured tree height. Stand dynamics in YN-EB1 showed similar trend to that in the present study site. Specifically, a reduction of stem density of *C. sieboldii* (Fig. S2-2) and basal area (a proxy for tree biomass) (Fig. S2-3) from 2004 to 2015. Given the similarities in stand structure and species composition

between YN-EB1 and the present study site, it is possible that similar phenomena, such as higher CWD production due to frequent TCs, are occurring. Moving forward, tracking tree height at other sites will be necessary to enhance the generalizability of the findings obtained in the present study.

2.4.3. Conclusion

This chapter analyzed tree inventory data in a stand in northern part of Okinawa Island to evaluate the impacts of frequent TCs on CWD production. The finding support hypothesis I proposed by Everham and Brokaw (1996) which expected that frequent TCs selectively remove specific trees, producing CWD until a certain threshold is reached. In the study site, frequent TCs mainly breaks stems of emergent tree and individuals with lower mechanical strength against wind gusts, producing CWD_{log}. This TC-induced tree decline possibly cause subsequent CWD_{snag} production. Such CWD production will temporarily dampen as susceptible trees are eliminated, but it will become prominent again as the forest regenerates. As a result, it has become clear that in this stand, frequent TCs suppresses biomass accumulation as the canopy height increases, and at the same time, CWD continues to be produced permanently in this study site.

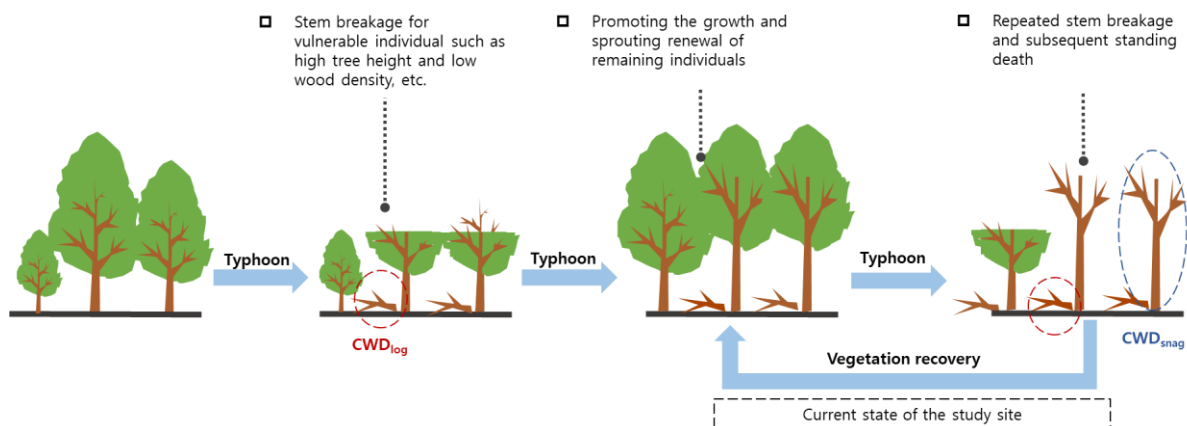


Fig. 2-6. Possible stand dynamics and CWD production in the study site

2.5. Supplemental materials

Table S2-1. Number of typhoons which approached (<300 km area) and landed on the study site.

Year	Occurrence	Approach	Landing
2010	14	4	1
2011	21	4	0
2012	25	8	3
2013	31	4	0
2014	23	6	1
2015	27	4	0
2016	26	3	0
2017	27	2	1
2018	29	8	2
2019	29	4	0

Table S2-2. The list of species-specific wood gravity (ρ , g cm⁻³). Tree species are sorted alphabetically by family name. Note that ρ values are obtained from Okinawa Prefectural Forest Resources Research Center, 2022.

Family name	Species name	ρ	Note
Aquifoliaceae	<i>Ilex goshiensis</i>	0.86	Value of <i>I. integra</i>
Aquifoliaceae	<i>Ilex integra</i>	0.86	
Aquifoliaceae	<i>Ilex liukiuensis</i>	0.86	Value of <i>I. integra</i>
Aquifoliaceae	<i>Ilex maximowicziana</i>	0.86	Value of <i>I. integra</i>
Araliaceae	<i>Dendropanax trifidus</i>	0.68	
Araliaceae	<i>Heptapleurum</i> <i>heptaphyllum</i>	0.37	
Celastraceae	<i>Microtropis japonica</i>	0.71	Overall average
Daphniphyllaceae	<i>Daphniphyllum teijsmannii</i>	0.60	
Ebenaceae	<i>Diospyros morrisiana</i>	0.68	
Elaeocarpaceae	<i>Elaeocarpus japonicus</i>	0.53	
Ericaceae	<i>Rhododendron tashiroi</i>	0.71	Overall average
Ericaceae	<i>Vaccinium wrightii</i>	0.71	Overall average
Fagaceae	<i>Castanopsis sieboldii</i>	0.51	
Hamamelidaceae	<i>Distylium racemosum</i>	0.91	
Lauraceae	<i>Cinnamomum doederleinii</i>	0.65	
Lauraceae	<i>Machilus thunbergii</i>	0.61	
Myricaceae	<i>Morella rubra</i>	0.71	
Myrtaceae	<i>Syzygium buxifolium</i>	0.98	
Oleaceae	<i>Osmanthus insularis</i>	0.94	
Phyllanthaceae	<i>Antidesma japonicum</i>	0.71	Overall average
Podocarpaceae	<i>Podocarpus macrophyllus</i>	0.59	
Primulaceae	<i>Ardisia quinqueгона</i>	0.99	Value of <i>P. macrophyllus</i>
Primulaceae	<i>Ardisia sieboldii</i>	0.99	Value of <i>P. macrophyllus</i>
Primulaceae	<i>Myrsine seguinii</i>	0.99	
Rosaceae	<i>Rhaphiolepis indica</i>	1.03	
Rosaceae	<i>Rhaphiolepis indica</i>	1.03	Value of <i>R. indica</i>
Rubiaceae	<i>Aidia canthioides</i>	0.77	Average of Rubiaceae family
Rubiaceae	<i>Diplospora dubia</i>	0.79	
Rubiaceae	<i>Gardenia jasminoides</i>	0.87	
Rubiaceae	<i>Tarenna kotoensis</i>	0.77	Average of Rubiaceae family
Rubiaceae	<i>Wendlandia formosana</i>	0.64	

Continued to next page

Table S2-2 (Continued).

Family name	Species name	ρ	Note
Sabiaceae	<i>Meliosma squamulata</i>	0.62	
Schisandraceae	<i>Illicium anisatum</i>	0.75	
Styracaceae	<i>Styrax japonicus</i>	0.59	
Symplocaceae	<i>Symplocos nakaharae</i>	0.69	
Symplocaceae	<i>Symplocos okinawensis</i>	0.61	Average of Symplocaceae family
Symplocaceae	<i>Symplocos prunifolia</i>	0.57	
Symplocaceae	<i>Symplocos prunifolia</i>	0.57	
Symplocaceae	<i>Symplocos stellaris</i>	0.61	Average of Symplocaceae family
Ternstroemiaceae	<i>Cleyera japonica</i>	0.72	
Ternstroemiaceae	<i>Eurya japonica</i>	0.78	
Ternstroemiaceae	<i>Ternstroemia gymnanthera</i>	0.76	
Theaceae	<i>Schima wallichii</i>	0.54	

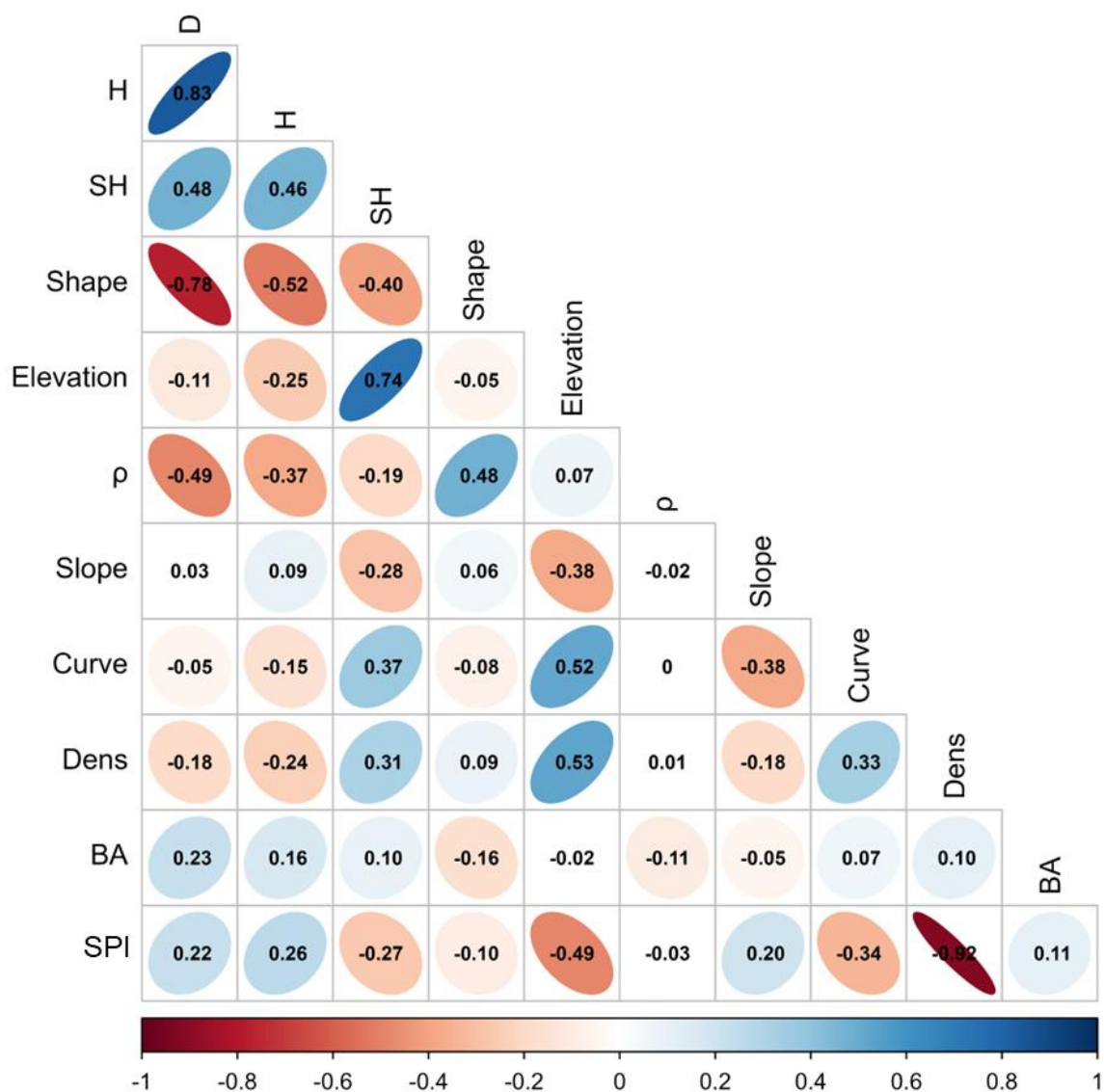


Fig. S2-1. Correlation matrix of tree character variables, topographic variables, and stand density variables. The numbers represent the correlation coefficients, and the ellipses represent significant correlations with a $p < 0.05$. Abbreviations: D, tree DBH; H, tree height; Shape, slenderness ratio; Elevation, elevation; ρ , species-specific wood gravity; Slope, slope angle; Curve, curvature; Dens, stem density; BA, basal area; and SPI, stand packing index.

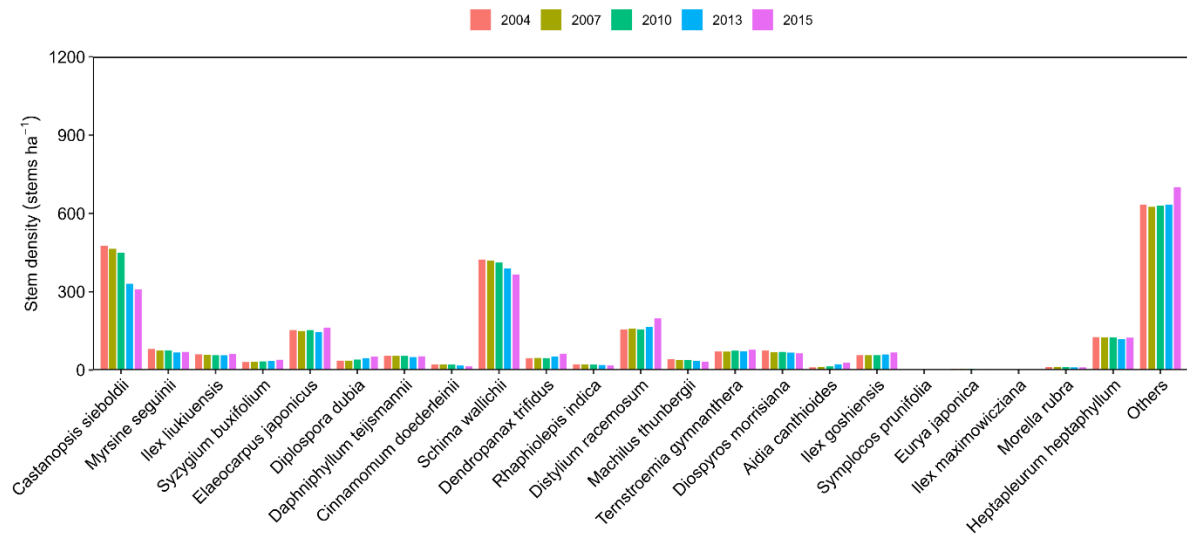


Fig. S2-2. Differences in stem density by species in neighboring 1 ha study site for trees with girth of breast height (GBH) >15 cm (i.e., DBH >4.78 cm). Data was obtained from monitoring sites 1000 (<https://www.biodic.go.jp/moni1000>).

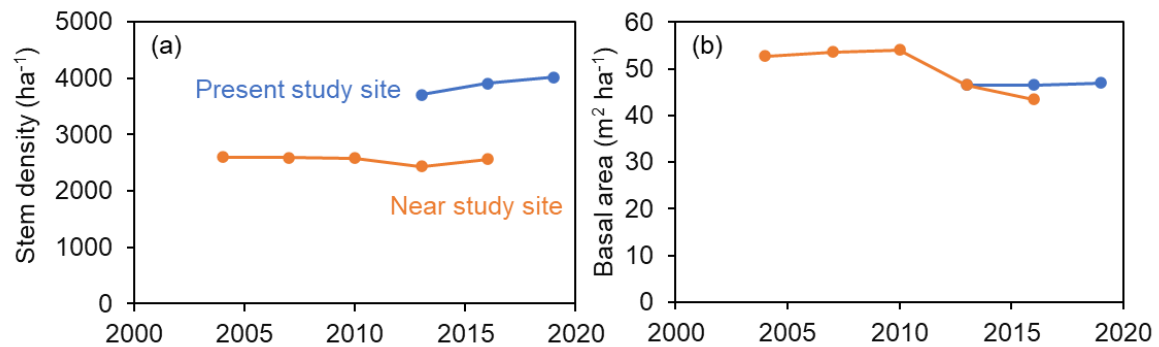


Fig. S2-3. Temporal trend of stem density and basal area in the present study site (blue line) and neighboring 1ha site (orange line). Given that data of neighboring site were collected for trees with GBH >15 cm, the data in the present study site was calculated without trees with GBH ≤15 cm.

Chapter 3: Impact of typhoon-produced coarse woody debris on the amount of stand-scale dead organic matter necromass and CO₂ efflux

3.1. Introduction

Plant biomass plays an important role in forest carbon (C) sequestration (FCS), even as dead organic matter (DOM) (Harmon et al. 1986; Xiong and Nilsson 1997; Berg and McClaugherty 2003). DOM is composed leaf litter, fine woody debris (FWD), and coarse woody debris (CWD). DOM contributed to forest C stocks and heterotrophic respiration (HR). For example, C stocks of DOM accounted for 2%–62% of aboveground C stocks (AGC) in forest ecosystems in Eurasia (Schepaschenko et al. 2017). Globally, HR from leaf litter and FWD accounted for 0.01%–78% of soil respiration (Bond-Lamberty and Thomson 2018). Several studies have shown that the HR from CWD was also equivalent to 2%–19% of soil respiration (Jomura et al. 2007; Ohtsuka et al. 2007; Gough et al. 2007; Tan et al. 2010). Therefore, it is essential to evaluate the contribution of DOM to C stocks and HR from DOM (R_{h_DOM}) for a better understanding of FCS.

It is well-known that characteristics in supply and decomposition rates differ among DOM types. For example, leaf litter and FWD are regularly generated by litterfall from the canopy, whereas CWD is often infrequently generated by wind, fire, disease, competition, and senescence (Jia-bing et al. 2005). CWD decomposes slower compared to leaf litter and FWD (Jens et al. 2007; Zhang et al. 6 2008). Generally, CO₂ efflux from a DOM with a faster decomposition rate is higher than that of a DOM with a slower decomposition rate (Makita and Fujii 2015; Mackensen and Bauhus 1 2003). Thus, the DOM supply and decomposition rate can determine necromass and, consequently, the R_{h_DOM} (Harmon, 2021). Therefore, evaluating necromass and R_{h_DOM} separately by DOM types is important to determine each DOM type's contributions to the total necromass and R_{h_DOM} .

CWD is also categorized by its location; downed CWD (CWD_{log}), such as fallen logs, are in contact with the ground, whereas standing CWD (CWD_{snag}), such as standing dead trees, are not (Swift et al. 1976; Christensen 1977; Yoda and Kira 1982). Necromass of CWD_{log} and CWD_{snag} are differ depending on the stand characteristics, including climate (Iwashita et al. 2013; Takeda and Takahashi 2020), topography (Palace et al., 2012), and stand type (i.e., stand

age and structure) (Kissing and Powers 2010; Pedlar et al. 2002). This variation of CWD_{snag} and CWD_{log} necromass reflect the differences in the amount of each produced and the rate of decomposition. It has been reported that proportion of CWD_{log} and CWD_{snag} production is differed via disturbance regime of the stand (Palace et al., 2012; Siitonen et al. 2000). For example, insect outbreak produces mainly CWD_{snag} (Jomura et al., 2007), while snow avalanches produces mainly CWD_{log} (Rigatti et al. 2024). Further, CWD_{log} shows faster decomposition rate than CWD_{snag} due to the higher water content inside of CWD (Hararuk et al. 2017). These studies suggest that it is necessary to examine CWD_{log} and CWD_{snag} separately for evaluating the role of CWD on FCS.

Spatial variability in DOM necromass is the key information to determine sizes and arrangements of sampling plots for stand-scale necromass estimates. Normally, larger sampling area is necessary for DOM with high spatial variability (Yoneda, 1982). For example, measurement area of CWD ($\geq 100 \text{ m}^2$) (Pedlar et al. 2002; Kissing and Powers 2010; Palace et al. 2012; Iwashita et al. 2013) is often larger than that of leaf litter and FWD ($\geq 1\text{--}5 \text{ m}^2$) (Kavvadias et al. 2001; Ugawa et al. 2012; Kuznetsov and Bobkova 2014). Given that R_{h_DOM} can be estimated using DOM necromass (Chambers et al. 2001; Uchida et al. 2005; Liu et al. 2006; Jomura et al. 2007; Gough et al. 2007), insufficient estimation of DOM necromass may leads inaccurate R_{h_DOM} estimate. Despite of this, there is limited information about the impact of spatial variation in DOM types on the DOM necromass and R_{h_DOM} estimates.

As shown in chapter 2, subtropical forests in Okinawa Island produce a high amount of CWD due to frequent tropical cyclones (TCs). In addition, it has been reported that TCs generate high amounts of leaf litter and FWD (Xu 1998; Alhamd and Hagihara 2004). In this forest with frequent TCs, we aimed to understand the characteristics of necromass and R_{h_DOM} for each DOM type and to develop an optimal sampling strategy to estimate necromass and R_{h_DOM} . For this aim, we measured necromass and R_{h_DOM} from aboveground leaf litter, FWD, CWD_{log}, and CWD_{snag} in the study site in chapter 2. We examined (1) the contribution of each DOM type to total necromass and total R_{h_DOM} from aboveground DOM, (2) the spatial distribution pattern of necromass of each DOM type, (3) the optimal sampling plot area and arrangement required for the accurate estimation of necromass and R_{h_DOM} based on the spatial distribution pattern of each DOM type in this forest, (4) the effect of spatial variability in each DOM type on the estimate error in total necromass and total R_{h_DOM} from aboveground DOM, and (5) the amount of forest C stocks and net C balance in this forest.

3.2. Methods

3.2.1. Sampling design for each type of dead organic matter

This study was conducted in a 2500 m² site in Yona Field (YF) on Okinawa Island. The detail of the study site was described in chapter 2. In the study site, sampling plots of four DOM types (i.e., leaf litter, FWD, CWD_{log}, and CWD_{snag}) were installed. Sampling plots were established with different areas and numbers in subplots for each DOM type (Table 4-1, Fig. 4-1). Leaf litter and FWD were collected in sampling plots with areas of 0.25 m² each, in 40 subplots (total area = 10 m²). For CWD_{snag} necromass estimate, standing CWD and suspended CWD were measured separately in the sampling plots with areas of 25 m² each, in 100 subplots (total area = 2500 m², area of the whole study plot). Downed CWD was sampled at three diameter size groups of 3–10 cm (CWD_{log_small}), 10–20 cm (CWD_{log_mid}), and >20 cm (CWD_{log_big}) according to the central diameter because it was considered to be sparsely distributed for larger diameter sizes (Yoneda, 1982). Specifically, CWD_{log_small} was collected in the sampling plots with areas of 3 m², in 40 subplots (total area = 120 m²), CWD_{log_mid} was collected in the sampling plots with areas of 12.25 m² each, in 40 subplots (total area = 490 m²), and CWD_{log_big} was collected in the sampling plots with areas of 25 m² each, in 100 subplots (total area = 2500 m², area of the whole study plot).

Table 3-1. The numbers and areas of the plots for dead organic matter (DOM) sampling.

DOM Type	Diameter (cm)	Sampling plots		
		Count	Each area (m ²)	Total area (m ²)
Leaf litter	-	40	0.25	10
Fine woody debris (FWD)	<3	40	0.25	10
Coarse woody debris (CWD)				
Downed CWD (CWD _{log})	>3			
Small	3–10	40	3.00	120
Middle	10–20	40	12.25	490
Big	>20	100	25.00	2500
Standing CWD (CWD _{snag})	>3	100	25.00	2500

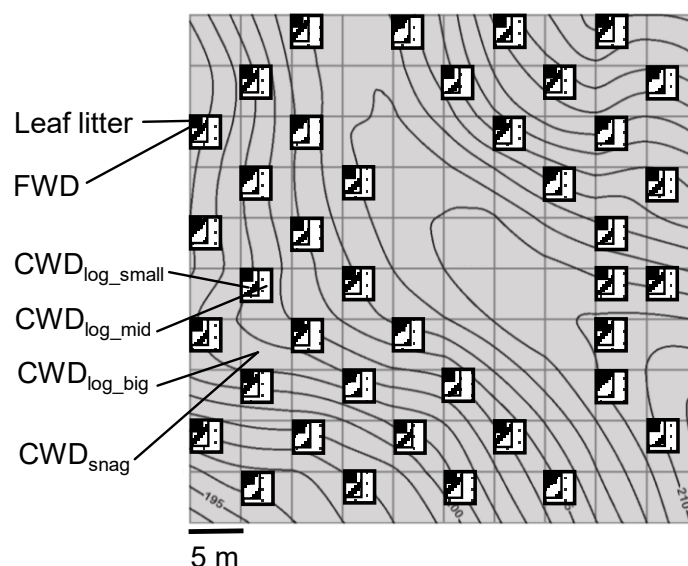


Fig. 3-2. Arrangements of the plots for dead organic matter (DOM) sampling. The DOM consisted of leaf litter, fine woody debris (FWD), and coarse woody debris (CWD). CWD was divided into downed CWD (CWD_{log}), which was grouped into three diameter classes (CWD_{log_small}, CWD_{log_mid}, and CWD_{log_big}), and standing CWD (CWD_{snag}).

3.2.2. Necromass estimation

The DOM necromass at each sampling plot was estimated as C stocks per area (g C m⁻²) by multiplying the dry mass of DOM per unit sampling area with the C content. Stand-scale necromass was estimated as the value averaged over that measured in all sampling plots. We

sampled the leaf litter, FWD, CWD_{log_small}, and CWD_{log_mid} at each sampling plot from June 30, 2019, to July 14, 2019. There were CWD_{log_small} or CWD_{log_mid} that lay down partially outside the boundary of the sampling plot. We cut them at the border of each sampling plot and sampled them as normal. After sampling, samples were dried using a dry oven under a constant temperature of 70°C for 2 days for leaf litter and FWD, and one week for CWD_{log_small} and CWD_{log_mid}. After drying, the dry mass was weighed.

The dry mass of CWD_{log_big} and CWD_{snag} was estimated by multiplying its stem volume with wood density. The stem volumes of CWD_{log_big} and CWD_{snag} were estimated using Smalian's formula for the volume of a cone (Baker and Chao 2011), as follows:

$$V = \frac{L(G_1 + G_2)}{2} \quad (\text{Eq. 3-1}),$$

where V is the volume (cm³), G_1 and G_2 are cross-section areas at both ends (cm²), and L is the length (cm). We measured the G_1 , G_2 , and L of CWD_{log_big} from September 18 to 25, 2019. Note that there were no CWD_{log_big}, which lay down across the multiple subplots. For CWD_{snag} with height ≤ 1.3 m, we measured the G_1 , G_2 , and L , as well as estimated V from September 18 to 25, 2019. For CWD_{snag} with height > 1.3 m, the volume was estimated by dividing it into two parts—one for those between the bottom and the 1.3 m height position and the other for those between the 1.3 m height position and the top. Each volume was calculated using Eq. 3-1. For the volume of the lower part, G_1 and G_2 were the diameter at the bottom and the 1.3 m height position ($D_{1.3}$), respectively, and L was the length from the bottom to the 1.3 m height position. For the volume of the upper part, G_1 and G_2 were the $D_{1.3}$ and diameter at the top, respectively, and L was the length from the 1.3 m height position to the top. At each sampling plot, the $D_{1.3}$ and tree height of CWD_{snag} with height > 1.3 m were measured. Diameters at the bottom and top were estimated using a taper function based on the $D_{1.3}$ and height, as follows:

$$\frac{D_H}{D_{1.3}} = \exp \left\{ \frac{a(H - 130)}{130} \right\} \quad (\text{Eq. 3-2}),$$

where D_H is the diameter (cm) at H cm height from the bottom, H is the length from the bottom to the estimated diameter height, $D_{1.3}$ is the diameter (cm) at 1.3 m height position, and a is the parameter; -0.093 for the top and -0.44 for the bottom. Eq. 3-2 represents a decrease in the diameter of the stem from the bottom to the top (Jessica et al. 2009). Parameter a was obtained based on the measured diameter of a standing dead tree, *Castanopsis sieboldii*, at the study site

(Fig. S3-1).

Wood densities (g cm^{-3}) for $\text{CWD}_{\log_big}$ and CWD_{snag} were determined by the decomposition levels. Decomposition levels were categorized into three levels based on the bark condition (Table S3-1). Wood densities for each decomposition level were obtained from five logs collected from a dead tree of *C. sieboldii* at the study site. The range of wood densities ($0.30\text{--}0.49 \text{ g cm}^{-3}$) in this study was comparable to those of previous studies (Chao et al. 2008; Lipan et al. 2008). Note that *C. sieboldii* accounts for approximately 65% of the total volume of all CWD_{snag} with height $>1.3 \text{ m}$ (Fig. S3-2), suggesting this species was representative of the CWD at the study site.

The C content per unit DOM dry mass was assumed at $0.50 \text{ (g C g}^{-1}\text{)}$ in this study based on values reported in previous studies, with C content per unit DOM dry mass at $0.46\text{--}0.53$ (Yoneda et al. 1977; Yoda and Kira 1982; Alhamd et al. 2004).

3.2.3. Spatial variability of each dead organic matter type and the required sampling numbers

The magnitude of spatial variability in each DOM type was evaluated by the coefficient of variation (CV) calculated from the necromass values at each sampling plot. The spatial distribution patterns were evaluated using semivariograms of necromass values (Gora et al., 2019), using Eq. 2-8. The analysis procedure were same as the analysis conducted in chapter 2. Note that the necromass value was transformed to $\log(x + 1)$ to remove the overdispersion before the analysis (Gora et al., 2019).

The number of sampling plots required to estimate necromass within an error d at an error rate α was calculated (Král et al. 2010) as follows:

$$N = \frac{t_{\alpha, n-1}^2 s^2}{d^2}$$

$$d = mD \quad (\text{Eq. 3-3}),$$

where N is the number of required sampling plots, $t_{\alpha, n-1}$ is Student's t value at an error rate α with degree of freedom $(n-1)$, s^2 is the population variance of necromass, and d is an error which is multiplied by the mean necromass m and accepted error D (no dimension, $0 < D \leq 1$). We obtained N for each DOM type when α was set at 0.05, and D was set at 0.1, 0.2, 0.3, 0.4, and 0.5, respectively. Then, we obtained the required sampling area by multiplying N , with α of 0.05 and D of 0.1 with the sampling area of each sampling plot.

3.2.4. CO₂ efflux measurements and annual value estimates

CO₂ efflux from leaf litter, FWD, and CWD_{log} was measured using the DOM of *C. sieboldii* five times between July to December 2019 at the study site. Leaf litter and FWD were collected on May 24, 2019. Then, we prepared 30 litter bags for leaf litter and FWD, respectively (bag size 20 × 15 cm, mesh size of 1 mm, 8–10 g dry mass of leaf litter and FWD) and placed them at the study site on June 30, 2019. Six leaf litter bags and six FWD bags were collected at each measurement campaign. Leaf litter and FWD were sampled from litter bags, and their CO₂ efflux was measured. After the measurement, leaf litter and FWD were dried at 70 °C for 2 days, and the dry mass of the samples without the bag was weighed. For the CO₂ efflux measurement from CWD_{log}, we obtained 17 logs from three individual dead trees of *C. sieboldii* at the study site on March 26, 2019 (Table S3-2). These logs were cut into a length of 1 m and a diameter of 5–18 cm. These decomposition levels were at level 1 during the study period. CO₂ efflux was measured for all 17 logs on each measurement day. The dry mass of logs was calculated by multiplying the volume of the log by the wood density of the disc partially taken from the log.

CO₂ efflux from leaf litter, FWD, and CWD_{log} was determined as the CO₂ increase per unit dry mass of DOM using an infrared gas analyzer (IRGA) and a closed chamber system, as follows:

$$R_g = \frac{dc}{dt} \times \frac{(V_{\text{system}} - V_{\text{sample}})}{V_{\text{air}}} \times \frac{273.15}{(273.15 + T_{\text{gas}})} \times \frac{60^2 \times 44.01 \times 10^{-3}}{W} \quad (\text{Eq. 3-4}),$$

where R_g is CO₂ efflux per unit dry mass of DOM (mg CO₂ kg⁻¹ h⁻¹), dc/dt is CO₂ increment per second (μmol mol⁻¹ s⁻¹), V_{system} is the volume of the chamber (0.99 L for leaf litter and FWD and 75 L for CWD_{log}), V_{sample} is the volume of measurement sample (L), V_{air} is the standard volume of the atmosphere (22.4 L mol⁻¹), T_{gas} is the temperature of gases (°C), and W is the dry mass of the measurement sample (kg). The V_{sample} of leaf litter and FWD were assumed to be zero. For leaf litter and FWD, an IRGA meter (LI-6400, LI-COR, Lincoln, NE, USA) and a soil respiration measurement chamber (6400-9, LI-COR, Lincoln, NE, USA) were used. For CWD_{log}, an IRGA sensor (GMP343, Vaisala, Helsinki, Finland) and an indicator (MI170, Vaisala, Helsinki, Finland) were used. Hourly data of soil temperature (°C) and soil volumetric water content (SVWC, %) at a depth of 5 cm were monitored in 2019 using water content

reflectometers (CS650, Campbell Scientific, Logan, UT, USA) and logged using programmable data logger (CR1000, Campbell Scientific, Logan, UT, USA), respectively.

CO₂ efflux from CWD_{snag} was measured for six individual standing CWD (Table S3-2). These samples were taken from three dominant tree species (three trees of *C. sieboldii*, two trees of *Schima wallichii*, and one tree of *Ilex liukiuensis*) at the study site. These trees died between 2013 and 2016. We measured the CO₂ efflux every 1 to 2 months in the period between December 2017 and October 2019 (total of 11 campaigns) using an LI-6400 and a soil respiration measurement chamber that was mounted on 2–4 collars, which were set onto the stem at a 1 m height. The efflux was represented per unit surface area (R_a) using the measured area:

$$R_a = \frac{dc}{dt} \times \frac{V_{\text{system}}}{V_{\text{air}}} \times \frac{273.15}{(273.15 + T_{\text{gas}})} \times \frac{1}{A} \quad (\text{Eq. 3-5}),$$

where R_a is CO₂ efflux per unit area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), V_{system} is 0.99 L, and A is the measurement area (0.0072 m²). The surface temperature was measured using an infrared radiation thermometer (Fluke-561, FLUKE, Everett, WA, USA) when CO₂ efflux was measured.

For estimating the annual R_g (g C g C⁻¹ yr⁻¹) of leaf litter, FWD, and CWD_{log}, models for CO₂ efflux for each DOM with environmental factors were established. First, we determined the environmental factors that should be used in the models for the annual estimate using an exponential regression model for soil temperature and a linear regression model for SVWC as follows:

$$R_g = a \exp(bT) \quad (\text{Eq. 3-6}),$$

$$R_g = cd\theta \quad (\text{Eq. 3-7}),$$

where T is the soil temperature (°C), θ is SVWC (%), and a , b , c , and d are model constants (Fig. S3-3). The constants in Eq. 3-6 and 3-7 were estimated using a least squares method. When the coefficient of determination (R^2) of either Eq. 3-6 or 3-8 was high (i.e., $R^2 \geq 0.25$), then the model was used for the annual R_g estimates. Here, soil temperature and SVWC were used for hourly measured data recorded in the study site (Fig. S3-4). When R^2 of both Eq. 3-6 and 3-7 was high, then CO₂ effluxes were estimated using both soil temperature and SVWC:

$$R_g = f \exp(hT) + (i\theta + j) \quad (\text{Eq. 3-8}),$$

where f , h , i , and j are model constants. These constants were estimated using the least squares

method. When R^2 of neither of Eq. 3-6 or 3-7 was not high (i.e., $R^2 < 0.25$), the environmental factors were not used for the annual R_g estimates, and the average for all measurement campaigns was used as the annual value. Similarly, the annual R_a ($\text{g C g C}^{-1} \text{ yr}^{-1}$) of CWD_{snag} was estimated using Eq. 3-6 with stem surface temperature of CWD_{snag} if R^2 of the model was high. Note that the surface temperature of CWD_{snag} was assumed to be equal to soil temperature based on the relationship between surface temperature and soil temperature (Fig. S3-3h). The units of annual R_g were converted from $\text{mg CO}_2 \text{ kg}^{-1} \text{ yr}^{-1}$ to $\text{g C g C}^{-1} \text{ yr}^{-1}$ using the C content per unit DOM dry mass (0.50 g C g^{-1}) and the ratio of molar masses of CO_2 and C.

The R_{h_DOM} from leaf litter, FWD, and CWD_{log} were estimated by multiplying the annual R_g and necromass. The R_{h_DOM} from CWD_{snag} was estimated by multiplying the annual R_a and the total surface area of CWD_{snag} per unit ground ($\text{m}^2 \text{ m}^{-2}$). The total surface area of CWD_{snag} was calculated by assuming the surface area of the individual CWD_{snag} to be a cone.

3.2.5. Potential impact of spatial variability of dead organic matter on stand-scale estimates

Although necromass and R_{h_DOM} estimates can have various sources of errors in measurement procedures, this study focused on the potential errors induced by the spatial variability of each DOM type in the total necromass and total R_{h_DOM} estimates. We defined the potential error induced by the spatial variability using the law of propagation. First, the propagated error of total necromass was calculated from the necromass and the standard deviation of the necromass of each DOM. Similarly, the propagated error of total R_{h_DOM} was calculated from R_{h_DOM} and the propagated error of R_{h_DOM} from each DOM. Here, the propagated error of R_{h_DOM} from each DOM was calculated by three values: annual R_g (or R_a), necromass (or surface area), and standard deviation of necromass (or surface area). Note that the estimated error of annual R_g (or R_a) was assumed to be zero because this study examined only spatial variability, and R_g (or R_a) was not measured with consideration of spatial variability. Second, the ratio of the square of the standard deviation of each DOM necromass to the square of propagated error of total necromass was calculated. Similarly, the ratio of the square of the propagated error of R_{h_DOM} for each DOM to the square of the propagated error of total R_{h_DOM} was calculated. The ratio was considered to be the potential error as the proportion of error derived from spatial variability of each DOM type to the estimated error of total necromass and

total R_{h_DOM} from aboveground DOM in this study.

3.3. Results

3.3.1. Necromass of dead organic matter

The total necromass of the aboveground DOM on a stand-scale was estimated at 1499.7 g C m⁻² at the study site (Table 3-2). It consisted of leaf litter (161.2 ± 116.0 g C m⁻², 11%), FWD (167.2 ± 121.3 g C m⁻², 11%), CWD_{log_small} (122.3 ± 132.7 g C m⁻², 8%), CWD_{log_mid} (181.7 ± 361.2 g C m⁻², 12%), CWD_{log_big} (59.3 ± 416.4 g C m⁻², 4%), and CWD_{snag} (807.9 ± 1397.8 g C m⁻², 54%) (Fig. 3-2). The total CWD (1171.2 g C m⁻²) accounted for 78% of the total necromass, and the CWD_{snag} accounted for 69% of the total CWD necromass. The necromass of CWD_{snag} was approximately five-fold higher than that of leaf litter and FWD.

Leaf litter and FWD were observed in all sampling plots, whereas CWD_{log} and CWD_{snag} were observed in 38 of the 40 plots and 66 of the 100 plots, respectively (Table 3-2). The CVs of the necromass for CWD_{log} and CWD_{snag} were 130% and 173%, respectively (Table 3-2). These were approximately two-fold higher than that of leaf litter (72%) and FWD (73%).

Table 3-2. Mean (g·C·m⁻²), standard deviation (SD), and coefficient of variation (CV, %) of necromass, and discovery rate for each dead organic matter (DOM) type.

DOM Type	Mean	SD	CV	Discovery rate ^a
Leaf litter	161.2	116.0	72	40/40
Fine woody debris (FWD)	167.2	121.3	73	40/40
Coarse woody debris (CWD)	1171.2			
CWD _{log} ^b	339.0	439.3	130	38/40
Small (3–10·cm)	122.3	132.7	109	38/40
Mid (10–20·cm)	181.7	361.2	199	19/40
Big (>20·cm)	59.3	416.4	702	3/100
CWD _{snag}	807.9	1397.8	173	66/100
Suspended	109.8	573.3	522	18/100
Standing	698.1	1146.9	164	63/100
Total	1499.7			

Superscript a: the discovery rate was calculated as the ratio of the number of sampling plots in which the target DOM type was present out of all the sampling plots.

Superscript b: note that statistical values for the total CWD_{log} were calculated from data on the 40 plots, where all diameter size classes of CWD_{log} were sampled. The total necromass of CWD_{log} (363.3 g C m⁻²) is not equal to a sum of the values for CWD_{log_small}, CWD_{log_mid}, and CWD_{log_big}.

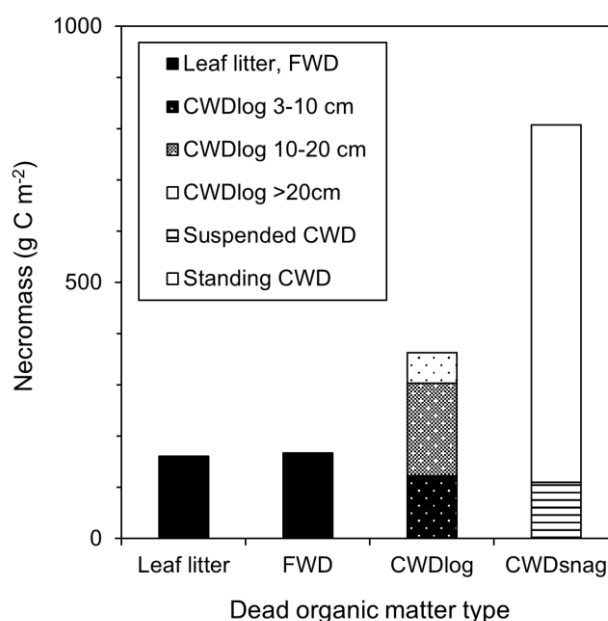


Fig. 3-2. Stand-scale necromass of leaf litter, fine woody debris (FWD), downed coarse woody debris (CWD_{log}), and standing CWD (CWD_{snag}).

3.3.2. Spatial dependence of necromass and sampling efforts for measuring necromass

Semivariogram analysis revealed that the strength and scale of spatial dependence of necromass varied with the DOM type (Table 3-3). The leaf litter analysis showed an exponential model with a range of 31 m, and its sill (0.04) was four-fold larger than its nugget (0.01). Similarly, the CWD_{snag} analysis showed a spherical model with a range of approximately 43 m, and its sill (2.30) was two-fold larger than its nugget (1.14). These results illustrate that leaf litter and CWD_{snag} had an autocorrelation, causing a spatial bias in the data in the range of 31 m and 43 m, respectively. The FWD and CWD_{log} analyses showed a linear model with a range of ≥ 50 m, yet these models were horizontal lines with equal values of their respective nugget and sill, suggesting that these DOM types did not have autocorrelation < 50 m. These results illustrate that leaf litter and CWD_{snag} were distributed locally, whereas FWD and CWD_{log} were randomly spread throughout the study site.

Table 3-3. Semivariogram models of the log (x + 1)-transformed necromass value for each DOM type.

Model	Leaf litter	FWD	CWD _{log}	CWD _{snag}
	Exponential	Linear	Linear	Spherical
Range (m)	31.20	– ^a	– ^a	43.30
Nugget	0.01	0.10	0.75	1.14
Sill	0.04	0.10	0.75	2.30
R ²	0.73	0.16	0.02	0.97

Superscript a: the range was not detected.

The number of required sampling plots at a 95% confidence level ($\alpha = 0.05$) and accepted error of 0.1 was higher than the actual number of sampling plots used in this study (Fig. 3-3). Leaf litter and FWD required 211 and 215 subplots, respectively, for DOM necromass estimation with a 95% confidence level ($\alpha = 0.05$) and accepted error of 0.1. These required numbers were five-fold higher than the actual number of sampling plots used here (40 subplots). The CWD_{log} and CWD_{snag} required 686 subplots and 1150 subplots, respectively. Each required number was 17- and 11-fold higher than the actual number of sampling plots used here (40 and 100 subplots, respectively). The required sampling area with a 95% confidence level ($\alpha = 0.05$) and accepted error of 0.1 for leaf litter, FWD, CWD_{log_small}, CWD_{log_mid}, and CWD_{log_big} were

$\geq 53 \text{ m}^2$; $\geq 54 \text{ m}^2$; $\geq 2058 \text{ m}^2$; $\geq 8404 \text{ m}^2$; and $\geq 42875 \text{ m}^2$, respectively. The required sampling area of CWD_{log} increased with diameter size. The required sampling area for CWD_{snag} was $\geq 7188 \text{ m}^2$ in each subplot, and four subplots were required, resulting in a total required sampling area of $\geq 28750 \text{ m}^2$. The plot arrangement of CWD_{snag} was required to be at a distance of $\geq 43 \text{ m}$.

3.3.3. Stand-scale CO₂ efflux estimate

The R_g from leaf litter was related to soil temperature and water content (Table 3-4, Fig. S3-3a, b), whereas R_g from FWD was related to only soil water content (Table 3-4, Fig. S3-3c, d). As there was no correlation between CWD_{log} and both soil temperature and SVWC (Fig. S3-3e, f), it was assumed that R_g from CWD_{log} did not differ temporally, and the average was used for the annual estimate (Table 3-4). The R_a from CWD_{snag} was related to surface temperature (Fig. S3-3g).

Leaf litter showed the highest annual R_g ($0.63 \text{ g C g C}^{-1} \text{ yr}^{-1}$), followed by FWD ($0.39 \text{ g C g C}^{-1} \text{ yr}^{-1}$) and CWD_{log} ($0.19 \text{ g C g C}^{-1} \text{ yr}^{-1}$) (Table 3-5). The total R_{h_DOM} from the aboveground DOM was estimated to be $320.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3-5). It consisted of leaf litter ($101.8 \text{ g C m}^{-2} \text{ yr}^{-1}$, 32%), FWD ($64.7 \text{ g C m}^{-2} \text{ yr}^{-1}$, 20%), CWD_{log} ($69.7 \text{ g C m}^{-2} \text{ yr}^{-1}$, 22%), and CWD_{snag} ($84.0 \text{ g C m}^{-2} \text{ yr}^{-1}$, 26%). The total CWD ($153.7 \text{ g C m}^{-2} \text{ yr}^{-1}$) accounted for 48% of the total R_{h_DOM} .

3.3.4. Potential errors derived from the dead organic matter types in stand-scale necromass and CO₂ efflux estimates

The proportion of potential error in the total necromass estimates was highest for CWD_{snag} (90%), followed by CWD_{log} (9%), FWD (0.7%), and leaf litter (0.6%) (Fig. 3-4). The total CWD accounted for the largest proportion of both total necromass (78%) and potential error in the total necromass estimates (99%) (Fig. 3-4). The proportion of potential error in the total R_{h_DOM} estimates was also highest for CWD_{snag} (68%), followed by leaf litter (12%), CWD_{log} (16%), and FWD (5%) (Fig. 3-4), even though the R_{h_DOM} of CWD_{snag} was lower than that of leaf litter (Table 3-5, Fig. 3-4). The total CWD accounted for the largest proportion for both total R_{h_DOM} (48%) and potential error in the total R_{h_DOM} estimates (83%) (Table 3-5, Fig. 3-4).

Table 3-4. The formula, root mean square percentage error (RMSPE), and coefficient of determination (R^2) of the CO₂ efflux estimate model.

Type	Formula	RMSPE (%) ^a	R^2
Leaf litter	$R_g = 0.000027 \times \exp(0.60T) + 1.27\theta + 31.67$	5.08	0.97
FWD	$R_g = 5.07\theta - 143.26$	2.60	0.72
CWD _{log}	$R_g = R_{g_average}$	4.20	–
CWD _{snag}	$R_a = 0.34 \times \exp(0.1T)$	2.05	0.86

Abbreviations: R_g : CO₂ efflux per unit mass (mg CO₂ kg⁻¹ h⁻¹); R_a : CO₂ efflux per unit area (μmol CO₂ m⁻² s⁻¹); R_{g_max} : maximum value of average R_g at each measurement day; $R_{g_average}$: average value of average R_g at each measurement day; T : soil temperature (°C); θ : soil volumetric water content (%).

Superscript a: RMSPE was calculated as the square root of the average of the squared ratio of the difference between the predicted and actual values divided by the actual value.

Superscript b: R^2 was not calculated because R_g from CWD_{log} was assumed to not differ temporally, and $R_{g_average}$ was used for the annual estimate.

Table 3-5. Annual CO₂ efflux per unit mass (R_g), annual CO₂ efflux per unit area (R_a), and stand-scale CO₂ efflux (R_{h_DOM}).

Type	Annual R_g	Annual R_a	Necromass ^a		Total surface area ^b		R_{h_DOM}	
	$g \cdot C \cdot g \cdot C^{-1} \cdot yr^{-1}$	$g \cdot C \cdot m^{-2} \cdot yr^{-1}$	$g \cdot C \cdot m^{-2}$	SD	$m^2 \cdot m^{-2}$	SD	$g \cdot C \cdot m^{-2} \cdot yr^{-1}$	Propagated errors ^c
Leaf litter	0.63	-	161.2	116.0	-	-	101.8	73.27
FWD	0.39	-	167.2	121.4	-	-	64.7	46.96
CWD			1171.2				153.7	
CWD _{log}	0.19	-	363.3	439.3	-	-	69.7	84.3
CWD _{snag}	-	974.15	807.9	1397.8	0.086	0.115	84.0	175.6
Total			1499.7	1474.8 ^d			320.2	213.4 ^d

Superscript a: mean and standard deviation (*SD*) of necromass were obtained from the values at each sampling plot.

Superscript b: mean and *SD* of total surface area were obtained from the values at each sampling plot.

Superscript c: propagated errors of R_{h_DOM} from each DOM type were calculated by a law of propagation of errors using three values: annual R_g (or R_a), necromass (or total surface area), and *SD* of the necromass (or total surface area).

Superscript d: using the law of propagation of errors, propagated error of total necromass was calculated from necromass and the *SD* of the necromass of each DOM type. The propagated error of total R_{h_DOM} was calculated from R_{h_DOM} and the propagated error of R_{h_DOM} from each DOM type.

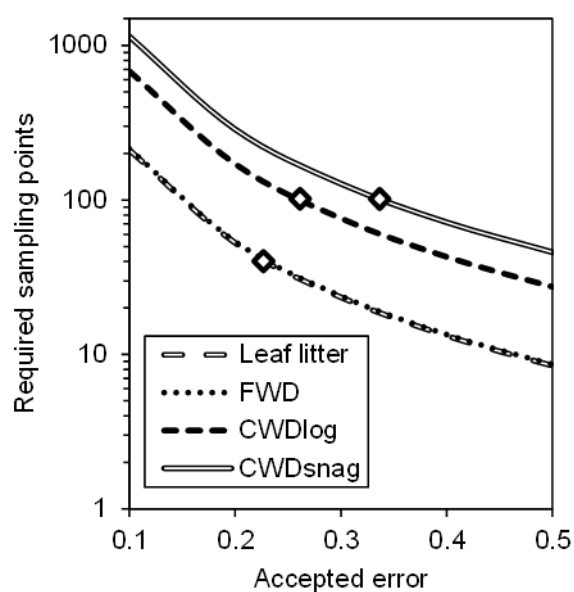


Fig. 3-3. Required number of sampling plots to estimate necromass at the 95% confidence level (error rate $\alpha = 0.05$) with an accepted error of 0.1–0.5. Diamonds (◇) indicate the intersection the number of sampling plots required to accurately determine the necromass estimate with the actual number of sampling plots in the study (40 or 100 subplots).

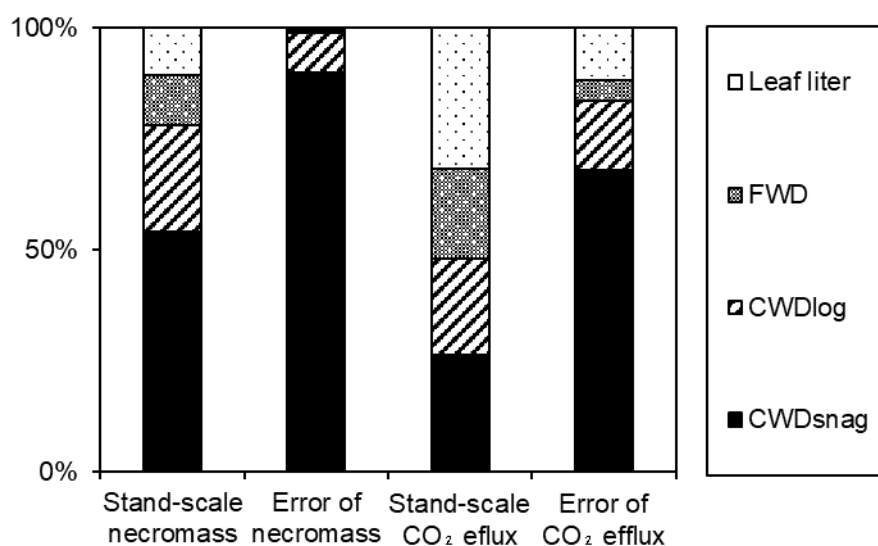


Fig. 3-4. Contribution of each DOM type to the total necromass and total CO₂ efflux (R_{h_DOM}) from aboveground dead organic matter and the proportion of potential error in the total necromass and total R_{h_DOM} estimates.

3.4. Discussions

3.4.1. Characteristics of necromass and CO₂ efflux from each dead organic matter type in the study site

The present study showed that CWD ($1171.2 \text{ g C m}^{-2}$) accounted for 78% of the total necromass of aboveground DOM (Table 3-2, Fig. 3-5). Data sets of C stocks in Eurasian forests reported CWD necromass that ranged from approximately 29–5577 g C m^{-2} , with an average of 712 g C m^{-2} (Schepaschenko et al., 2017). The CWD necromass in the present study was approximately 1.5-fold higher than the overall average. The CWD_{snag} accounted for 69% of the total CWD at the study site (Table 3-3, Fig. 3-4), although previous studies reported that CWD_{snag} accounted for $\leq 50\%$ of the total CWD in most forests (Sollins et al., 1980; Harmon et al., 1986; Pedlar et al., 2002; Kissing and Powers, 2010; Palace et al., 2012; Schepaschenko et al., 2017). Jomura et al. (2007) reported that CWD_{snag} accounted for approximately 70% of the total CWD in a temperate broad-leaved secondary forest where many trees were considered as standing death due to widespread pest infestation. Similarly, by considering the results of chapter 2, our result showed that high CWD_{snag} production due to frequent TCs leads to high necromass of CWD_{snag} in the study site.

The R_{h_DOM} from CWD accounted for 48% of the total R_{h_DOM} from aboveground DOM (Fig. 3-4). It also accounted for 8% of soil respiration estimated at 1959 $\text{g C m}^{-2} \text{ yr}^{-1}$ in the study site (Matsumoto et al. 2023). This result suggested that CO₂ efflux from CWD (i.e., R_{h_CWD}) was not negligible for the C efflux from the ecosystem. Although the R_{h_CWD} was not estimated in many previous studies (Liu et al. 2006; Zeng et al. 2009; Harmon et al. 2011), some studies have reported the contribution of CWD to soil respiration. For example, the ratio of R_{h_CWD} to soil respiration is 2%–19% in temperate forests (Gough et al., 2007; Jomura et al., 2007; Ohtsuka et al., 2007) and 15% in tropical seasonal rain forests (Tan et al., 2010). The contribution of CWD to soil respiration was comparable to those of previous studies despite the high CWD necromass.

The R_{h_DOM} can change not only with DOM type but also with DOM quality and decomposition level. Previous studies have shown that R_{h_DOM} varied with DOM qualities such as nitrogen and lignin concentrations (Coûteaux et al. 1995; Zhou et al. 2007; Makita and Fujii 2015) and the differences in DOM qualities among tree species caused the CO₂ efflux variation (Osono and Takeda 2004; Cornwell et al. 2008). It has also been reported that the R_{h_CWD}

increased with decomposition levels (Yoneda et al. 1977; Russell et al. 2015). Thus, further studies examining the effects of different DOM qualities and different decomposition levels on CO₂ efflux, will improve our ability to estimate R_{h_DOM} .

3.4.2. Carbon stock and net ecosystem production in the study site

Based on the results of this chapter with those of chapter 2, the AGC at the present study site was roughly estimated to be 8684 g C m⁻² (Fig. 3-5). This AGC consisted of overstory stem biomass in 2019 (7185 g C m⁻², 83% of total AGC), leaf litter and FWD (328 g C m⁻², 4%), and CWD (1171 g C m⁻², 14%). The stand age of the present study site was estimated as 40–80 years because this site was heavily logged until 1940 and affected by selective logging until 1980 (Hirata et al., 1979). The AGC in the present study site was intermediate between that of similar-aged stands (50–90 years old, 6223 g C m⁻²) and mature stands (>100 years old, 9872 g C m⁻²) reported in intact subtropical forests in China (Fang et al. 2007; Sun and Guan 2014) (Fig. 3-5). One reason for this result is attributed by the relatively higher C stock of CWD in the present study site (Fig. 3-5).

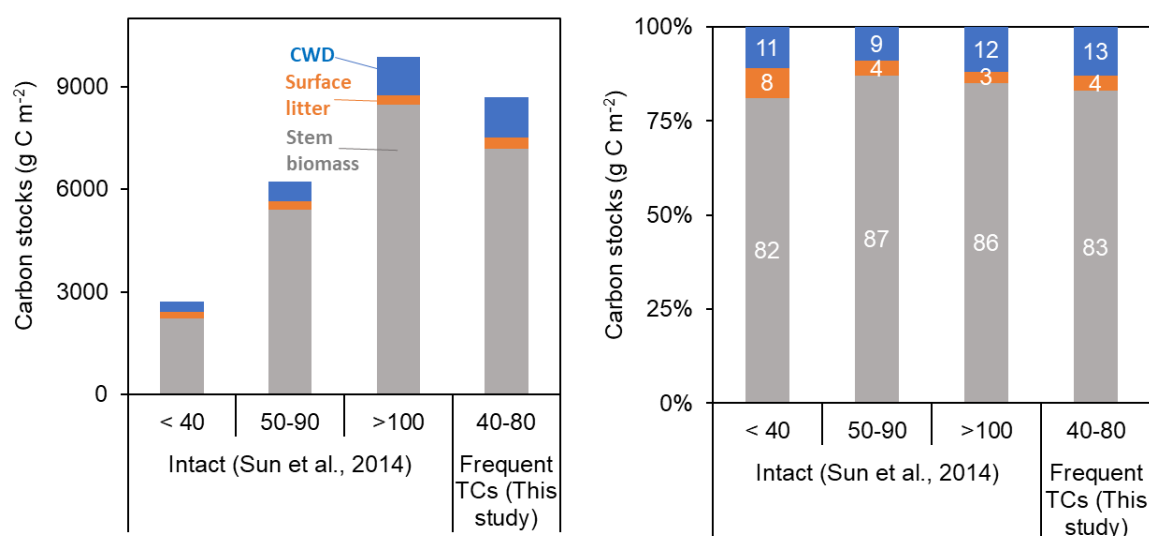


Fig. 3-5. Aboveground C stocks (left) and relative contribution (right) of each component among intact subtropical forests in China (Sun and Guan, 2014) and a present study site. The value in the X-axis shows the stand ages in each stand. Note that stem biomass in intact forests was converted from total biomass using the stem biomass/ total biomass ratio reported by Fang et al. (2007).

By combining the results of this chapter with literature values, the net ecosystem productivity (NEP) at the present study site was roughly estimated as follows. The above-ground net primary production (ANPP) of the present study site in 2013–2019 was estimated to be 473 g C m⁻² yr⁻¹. ANPP was derived from litterfall (323 g C m⁻² yr⁻¹) (Matsumoto et al., 2023) and annual stem growth (150 g C m⁻² yr⁻¹, Fig. 3-6, data are shown in chapter 2). Since there was no data available for belowground net primary production (BNPP), it was estimated using the BNPP/ANPP ratio for subtropical forests from a global dataset (BNPP = 0.42 × ANPP = 0.42 * 473 ÷ 199 g C m⁻² yr⁻¹) (Xiao et al. 2023). Then, the total NPP was estimated to be 672 C m⁻² yr⁻¹. HR was estimated to be 502 g C m⁻² yr⁻¹, which included HR from DOM (i.e., R_{h_DOM} , 321 g C m⁻² yr⁻¹) and HR from soil organic matter (SOM) (i.e., R_{h_SOM} , 688 g C m⁻² yr⁻¹). The R_{h_SOM} was obtained by substituting the annual soil respiration of the study site (1959 g C m⁻² yr⁻¹) (Matsumoto et al., 2023) into the HR estimation formula using the global dataset [$\ln(R_{h_SOM} + R_{h_LL} + R_{h_FWD}) = 1.22 + 0.73 \times \ln(\text{soil respiration})$] (Bond-Lamberty et al. 2004), and then subtracting HR from leaf litter and FWD (i.e., $R_{h_LL} + R_{h_FWD}$, 167 g C m⁻² yr⁻¹) from that. As a result, the NEP of the present study site was estimated to be -346 g C m⁻² yr⁻¹, suggesting this study site was a net C source. The calculated NEP was 190% lower than the average NEP (362 g C m⁻² yr⁻¹) estimated for other subtropical forests in East Asia (Yu et al. 2014).

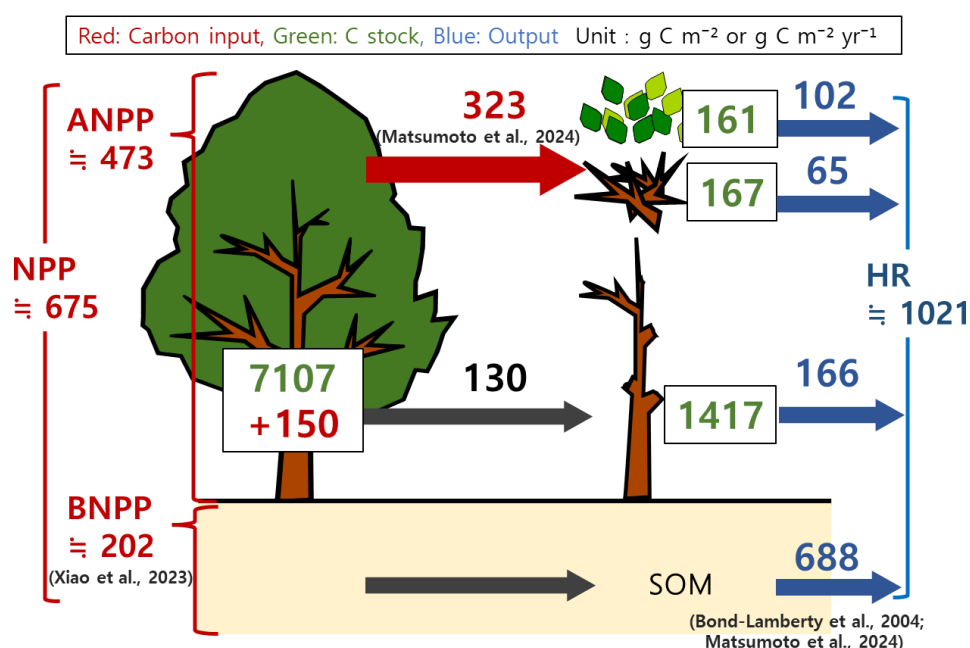


Fig. 3-6. Diagram of C stocks and flux in the study site.

The estimated AGC and NEP emphasize the feature of the frequent TCs impact on FCS. As discussed in chapter 2, frequent TCs caused significant stem breakage and tree mortality in the present study site, leading to substantial production of CWD. This CWD increased HR, which can decrease NEP. Contrastingly, the stored C in CWD contributed to maintaining the AGC. The reduction in NEP associated with TCs has also been reported at other research sites. For example, in a cool-temperate forest in Japan, NEP was continuously measured from 1999 to 2021 using the eddy covariance method (Murayama et al. 2024). Their results showed that a single TC in 2004 caused NEP to drop by 66% ($96 \text{ g C m}^{-2} \text{ yr}^{-1}$), from an average value of $287.5 \pm 74.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ (based on data from 1999–2021, excluding 2004). A key difference between their study site and the present study site is the frequency of TCs. At their study site, no other year besides 2004 experienced exceeding hourly maximum wind speeds of 10 m s^{-1} . Consequently, NEP at their site recovered to pre-TC levels within eight years (Murayama et al., 2024). In contrast, at the present study site, winds exceeding 10 m s^{-1} occur annually (see Fig. 2-1 in chapter 2). This suggests that recovery of NEP and further increases in AGC in the present study site is unlikely under current conditions.

3.4.3. Implications for sampling design

The magnitude of spatial variability in the necromass was greatest for CWD_{snag} , followed by CWD_{log} , FWD, and leaf litter (Table 3-2). Accordingly, the required sampling area for leaf litter and FWD ($53\text{--}54 \text{ m}^2$) was five-fold larger than the actual sampling plot, whereas the required sampling area of CWD ($2058\text{--}42875 \text{ m}^2$) was 11–17-fold larger than the actual sampling plot (Fig. 3-3). Gora et al. (2019) reported that a survey area of 63000 m^2 and 56000 m^2 is necessary for necromass estimation of a standing dead tree with a diameter of $\leq 20 \text{ cm}$ and $>20 \text{ cm}$, respectively, in a tropical forest. Král et al. (2010) also suggested that an area $\geq 127200\text{--}280000 \text{ m}^2$ is needed to estimate the CWD volume with a diameter $\geq 10 \text{ cm}$ in European forests. These studies suggest that the required sampling area for CWD differs from that of the study sites used here because of different spatial variability. Various causes of tree death can induce spatial variability in CWD, resulting in difficulties in consistently understanding the optimal sampling strategy for accurate estimates.

At the present study site, spatial autocorrelation existed for leaf litter with a range of 31 m and CWD_{snag} with a range of 42 m, in contrast, no autocorrelation was found for FWD and CWD_{log} (Table 3-3). The spatial autocorrelation of CWD_{snag} necromass was inconsistent with

the results in chapter 2, which shows no spatial autocorrelation for CWD_{snag} production. This discrepancy may be explained by the effect of topography on CWD decomposability, such as the difference in soil moisture between ridges and valleys (Clark et al. 2002). Similarly, the spatial autocorrelation of leaf litter necromass may be attributed to topographic differences in leaf litter production and its decomposability (Orndorff and Lang 1981; Gale and Barford 1999). The present study did not measure the effects of topography on DOM decomposition, future study is required to test this possibility. Besides, previous studies showed leaf litter, and FWD was spatially autocorrelated with a range ≤ 5 m in planted pine forests (Penne et al. 2010). It has also been reported that the spatial distribution of CWD does not show spatial autocorrelation in tropical forests (Péllico et al. 2018). These studies suggest that the spatial autocorrelation of DOM depends on topography, forest type, and DOM type. When spatial autocorrelation was observed for sampling DOM, the distances between sampling plots must be considered. Ultimately, assuming that the study site has high spatial representativeness of the forest ecosystem, the distance between sampling plots would need to be 31 m and 42 m, respectively, to sample leaf litter and CWD_{snag} without data bias occurring due to spatial autocorrelation. Note that this study has not measured spatial variations of necromass at ≤ 5 m distance; therefore, further measurements in this study area are needed to verify the spatial autocorrelation at ≤ 5 m.

This study showed that spatial variability in each DOM type affected not only the accuracy of necromass estimates, but also the accuracy of R_{h_DOM} estimates (Fig. 3-4). In particular, the spatial variability in CWD was higher than those of leaf litter and FWD, resulting in a higher influence of CWD on both necromass and R_{h_DOM} estimates. This suggests that an accurate estimate of CWD necromass is important for R_{h_DOM} estimation. In addition, CWD_{snag} considerably influenced the necromass and R_{h_DOM} estimates because of the high ratio of total necromass, despite the decomposition rate of CWD_{snag} being slower than that of CWD_{log} (Hararuk et al., 2017). It is also necessary to consider the effect of CWD_{snag} on necromass and R_{h_DOM} estimates, especially in forests with frequent TCs.

3.4.4. Conclusions

This chapter quantified necromass and R_{h_DOM} from leaf litter, FWD, CWD_{log}, and CWD_{snag} separately and estimated the total necromass and total R_{h_DOM} from these DOM types in an Asian subtropical forest located in a maritime subtropical climate. Among all aboveground DOM types, CWD accounted for the largest contribution of the total necromass and total R_{h_DOM}

estimates. This high CWD necromass mitigated AGC decrease due to the biomass loss via TCs, while high HR from CWD decreased NEP, leading to a net C source in the present study site. Further, spatial variability in necromass was also highest for CWD, especially for CWD_{snag}. As a result, CWD was a major source of error in total necromass and total R_{h_DOM} estimates.

3.5. Supplemental materials

Table S3-1. Wood densities of the coarse woody debris by decomposition levels.

Decomposition level	Bark conditions	Density (g cm ⁻³)
1	The outer bark and inner bark remain.	0.49
2	The outer bark is mostly shed or gone. The inner bark remains.	0.39
3	The shape of the wood is discernible, but the outer and inner bark is shed or gone.	0.30

Table S3-2. Tree species, diameter at breast height (DBH), height, and decomposition level of CO₂ efflux measurement samples of downed coarse woody debris (CWD_{log}) and standing or suspended coarse woody debris (CWD_{snag}).

No.	Type	Tree species	DBH (cm)	Height (m)	Decomposition level at measurement time	
					Start	End
1	CWD _{log}	<i>Castanopsis sieboldii</i>	10.9	8.0	1	1
2	CWD _{log}	<i>Castanopsis sieboldii</i>	12.0	10.4	1	1
3	CWD _{log}	<i>Castanopsis sieboldii</i>	17.5	11.8	1	1
4	CWD _{snag}	<i>Castanopsis sieboldii</i>	15.8	10.8	1	2
5	CWD _{snag}	<i>Castanopsis sieboldii</i>	16.6	6.2	1	1
6	CWD _{snag}	<i>Castanopsis sieboldii</i>	21.9	12.0	1	1
7	CWD _{snag}	<i>Schima wallichii</i>	17.9	9.2	1	2
8	CWD _{snag}	<i>Schima wallichii</i>	20.6	8.6	1	1
9	CWD _{snag}	<i>Ilex liukuensis</i>	21.8	12.3	1	1

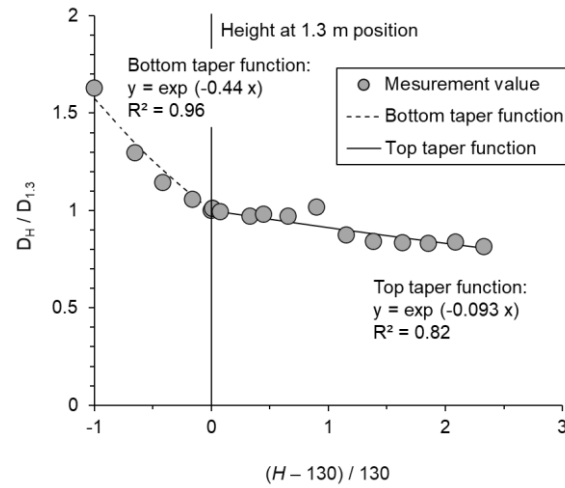


Fig. S3-1. Taper function of standing or suspended coarse woody debris (CWD_{snag}). This taper function was created by cutting logs from a standing dead tree of *Castanopsis sieboldii* ($D_{1.3}$, 18.2 cm; height, 5.9 m) and recording the diameter and length of each log.

Abbreviations: D_H : the diameter (cm) at H cm height; H : the length (cm) from the bottom to the estimated diameter height; $D_{1.3}$: diameter (cm) at a 1.3-m height position. The x-axis shows the relative height of the estimated diameter height relative to 1.3-m height.

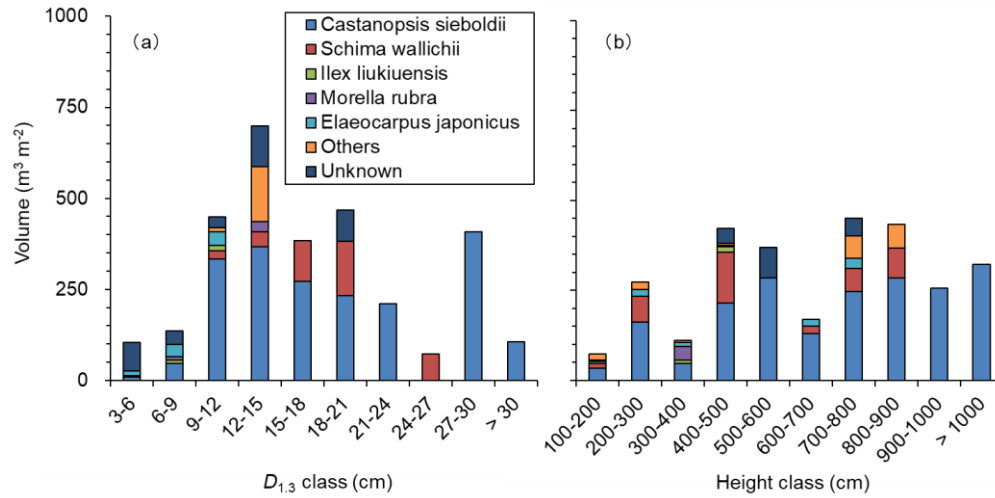


Fig. S3-2. Volume histogram of standing or suspended coarse woody debris (CWD_{snag}) with height > 1.3 m by diameter at 1.3 m height position ($D_{1.3}$ class (a) and Height class (b). Legends indicate the scientific name of the dominant tree species, other species (Others), and species that were indistinguishable (Unknown). *Castanopsis sieboldii* was widespread in all class widths, both in the $D_{1.3}$ class and Height class. It accounted for 65% of the total volume (3034.22 m³ m⁻²).

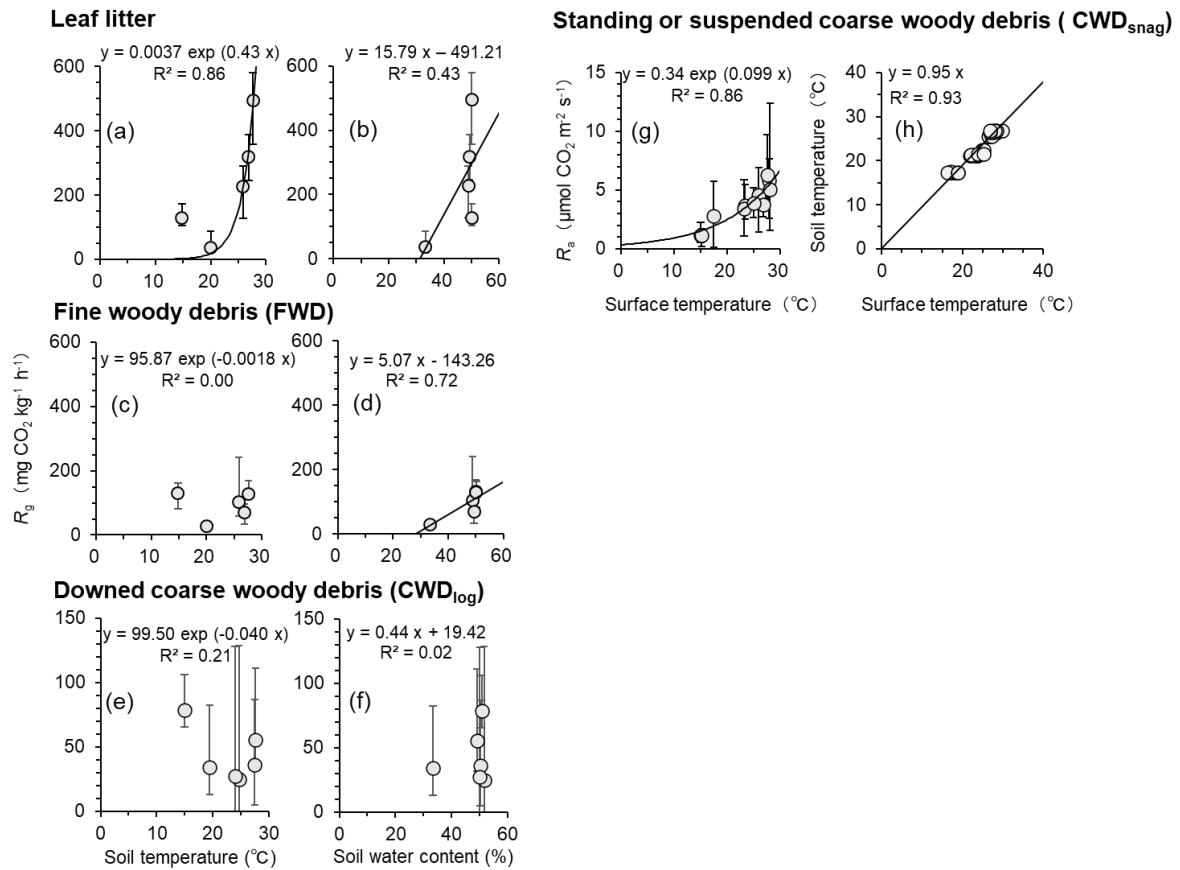


Fig. S3-3. Relationships between CO₂ efflux (R_g and R_a) and soil temperature, surface temperature, and soil volumetric water content of each dead organic matter (DOM) type (a–g) and the relationships between surface temperature and soil temperature (h). The circle symbol with bars indicates the mean, minimum, and maximum value at each measurement day. Leaf litter showed (a) an exponential relationship with soil temperature and (b) a linear relationship with soil water content. Fine woody debris (FWD) showed (c) no relationship with soil temperature and (d) a linear relationship with soil water content. Downed CWD (CWD_{log}) showed no relationship with both (e) soil temperature and (f) soil water content. Standing or suspended coarse woody debris (CWD_{snag}) showed (g) an exponential relationship with surface temperature; and (h) the surface temperature and soil temperature showed linear relationships with a correspondence of approximately 100:95.

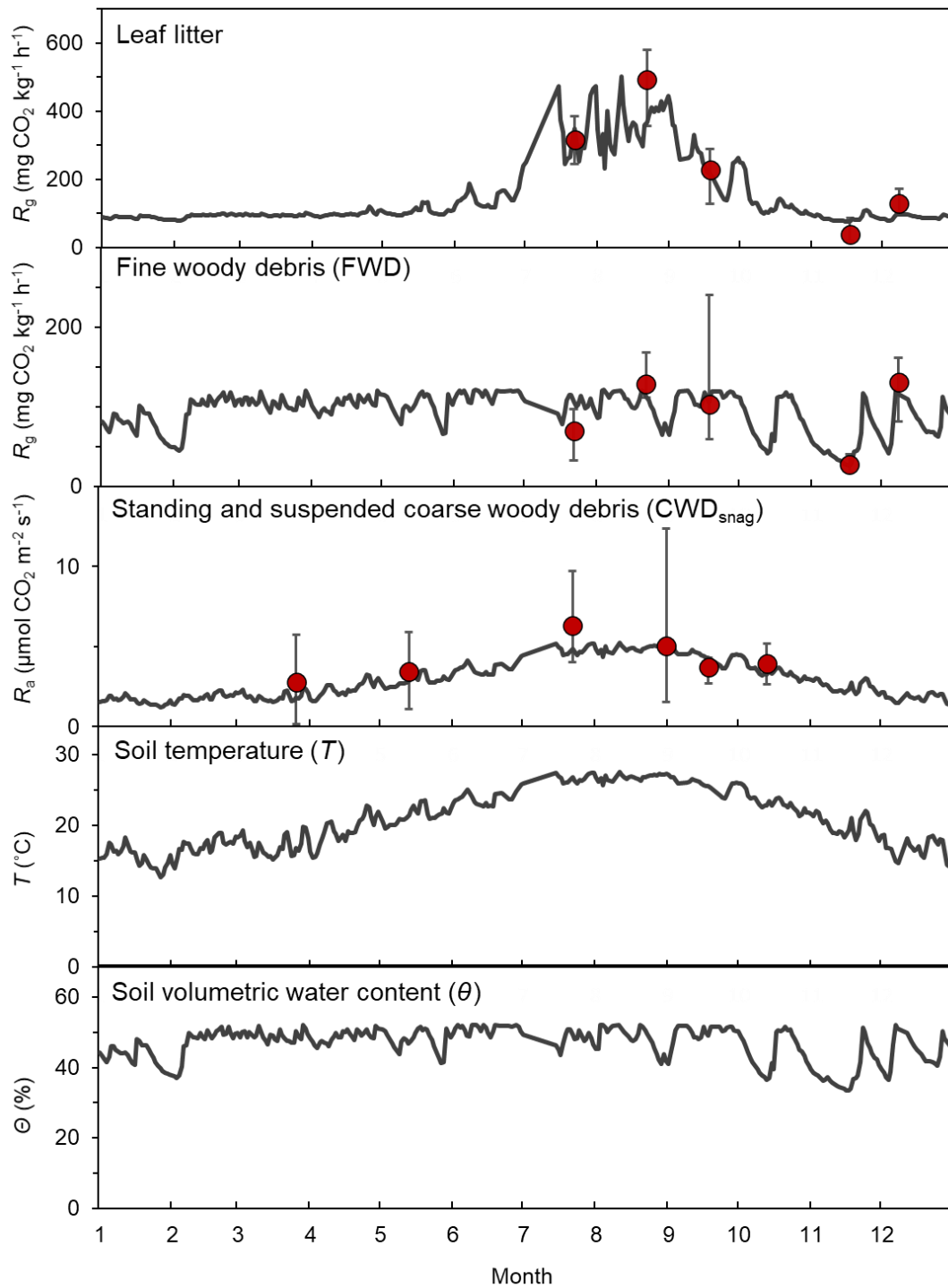


Fig. S3-4. Changes in estimated CO₂ efflux of each DOM type (R_g and R_a), measured soil temperature (T), and measured soil volumetric water content (θ) during 2019. The circle symbol with bars indicates the mean, minimum, and maximum value at each measurement campaign.

Chapter 4: Effects of soil erosion due to prolonged deer herbivory on tree growth

4.1. Introduction

Soil erosion, a process of topsoil removal by water and wind, causes soil degradation, which includes changes in the physical, chemical, and biological properties of the soil (Lal 2001; Mitchell et al. 2022). In forest ecosystems, understory vegetation and surface litter layer usually cover the topsoil and prevent soil erosion (Borrelli et al. 2017; Yamashita et al. 2022). However, in recent years, populations of ungulates such as deer have increased in forests in Europe (Côté et al. 2004), North America (Tape et al. 2016), and Asia (Takatsuki 2009). Herbivory by overpopulated ungulates (hereafter overbrowsing) has resulted in the loss of understory vegetation and thus promoted the soil erosion rate in montane slopes (Mekuria et al. 2007; Zheng et al. 2008; Labrière et al. 2015; Mizuno et al. 2021). Soil erosion and degradation have been reported to reduce plant productivity in agricultural ecosystems (den Biggelaar et al. 2003). Flores et al. (2020) reviewed literature for forest ecosystems and hypothesized that soil erosion hinders stand regeneration after forest fires in central Amazonia. However, to our knowledge, there is no direct evidence that soil erosion reduces tree growth. Therefore, quantifying soil erosion and its impacts on tree growth is important to evaluate the impacts of overbrowsing on forest carbon (C) sequestration (FCS) in montane forests.

Soil erosion occurs sporadically in forest ecosystems because of spatiotemporal variations in biotic and abiotic factors, such as canopy architecture development (Seitz et al. 2016), litter layer accumulation (Miura et al. 2015), and topography (Phinzi and Ngetar 2019). Hence, spatial heterogeneity of soil erosion within the same forested area must be considered when studying the effects of soil erosion on tree growth. Tree roots exposed by soil detachment (hereafter exposed roots) (Bodoque et al. 2005) are a useful index to evaluate spatial variation in soil erosion status among individuals of the same species (Stoffel and Bollschweiler 2008). Exposed root height (ERH), the vertical length from exposed roots surface to the soil surface, measured as the degree of eroded soil depth, is used as a surrogate for estimating the soil erosion rate (Hupp and Carey 1990; Pelfini and Santilli 2006; Pérez-Rodríguez et al. 2007; Chartier et al. 2009). The ERH surrounding trees may explain the relationships between soil erosion and tree growth at individual tree scale.

Topsoil removal via erosion reduces the soil water and nitrogen (N) contents (Andraski and Lowery 1992; Kort et al. 1998; Yao et al. 2019). In addition, root exposure via erosion leads to root injury and death (Pittermann and Sperry 2003; Cleavitt et al. 2008). Tree growth is reduced by a decline in soil water and N (Gessler et al. 2017; Hevia et al. 2019) as well as root injury and death (Arbellay et al. 2012; Comerford et al. 2013). Accordingly, it can be inferred that increased ERH will cause water and nutrient limitations, reducing mature tree growth. The assumption that water and/or N limitation drives tree growth reduction via soil erosion can be tested by quantifying physiological indicators such as water use efficiency (WUE) and N use efficiency (NUE) (Shortle et al. 2000; Cherubini et al. 2021). Water limitation causes closure of the stomata of tree leaves and hence increases intrinsic WUE (iWUE), which is calculated from the stable C isotope ratio ($^{13}\text{C}/^{12}\text{C}$ ratio) of stem wood (Farquhar and Richards 1984). Thus, a negative relationship between iWUE and stem growth rate was used to support the idea that water limitation reduces tree growth (Wieser et al. 2018). Similarly, N limitation decreases N concentration in a litter, increasing N use efficiency (NUE) (Tateno and Takeda 2010). Following this, the negative relationship between NUE and leaf production was used to reveal that soil oligotrophy reduces tree growth (Hikosaka 2005).

The tree growth reduction due to erosion is expected to occur after the degradation of the understory vegetation. Temporal changes in tree growth obtained from tree rings provide the useful information for detecting environmental factors that limit tree growth. For example, whether drought (Yadav et al. 2015) and air pollution (Kobayashi et al., 1998, Nöjd et al., 1996) reduce tree growth has been tested by comparing the timing of reduced annual precipitation and increased industrial activity, respectively, with the timing of the decline of annual ring growth. Generally, it is difficult to obtain long-term monitoring data on soil erosion (Boix-Fayos et al., 2006). As an alternative, a causal relationship between soil erosion and tree growth could be supported by examining whether the occurrence of the soil erosion driver (i.e., period of understory degradation) coincides with the initiation of the tree growth reduction.

Severe soil erosion has been observed in forest ecosystems on the mountain slopes of southern Kyushu Island, Japan (Enoki and Takahashi 2016; Abe et al. 2022; Hishi et al. 2022), due to a combination of heavy Asian monsoon rainfall (Panagos et al. 2017) and the consumption of understory vegetation by overpopulated Japanese sika deer (*Cervus nippon*) since 1980 (Saruki et al. 2004). The Japanese beech tree (*Fagus crenata*) in this area is a genetically valuable population within the western and southern limits of beech distribution in

Japan (Fujii et al. 2002). The Ministry of Agriculture, Forestry, and Fisheries in Japan considers beech trees on the Kyushu Island a conservation target and is trying to maintain the population (Kyushu Regional Forest Office, 2018). Despite conservation efforts, tree mortalities and reduced amount of crown leaves have recently been observed in several beech forests where understory vegetation has disappeared (Kotani et al. 2007; Hokusatsu Forest Office 2009; Kyushu Regional Forest Office 2019).

This chapter explored the influence of sporadic soil erosion following understory degradation on the beech growth reduction on southern Kyushu Island. To this end, 12 beech trees growing in the same forest area with different extents of soil erosion were targeted. We evaluated eroded soil depth by measuring ERH under individual beech trees. We also measured beech growth, temporal trend of stem growth, soil properties, and beech physiological conditions including iWUE and NUE at the individual tree scale. Subsequently, we tested the following hypotheses: (1) increasing ERH reduces beech growth (i.e., negative relationship between ERH and leaf, stem, and fine root production), (2) beech growth reduction has occurred since the time the understory was degraded and lost (i.e., stem basal area increment (BAI) declined after understory degradation), and (3) increasing iWUE and/or NUE reduces beech growth (i.e., negative relationship between iWUE and stem growth and/or NUE and leaf production).

4.2. Methods

4.2.1. Study site and trees

This study was conducted at Mt. Sanpo (32°22'30"N, 131°11'31"E, 1402–1451 m a. s. l.) in the Kyushu University Shiiba Research Forest (SRF) (Fig. 4-1). This study site is dominated by Japanese beech trees (*F. crenata*) which sparsely distributed and creates an open forest canopy (Fig. 4-2a). The understory vegetation at the study site had begun to decrease since the 1980s (Murata et al. 2009) and disappeared by 2003 (Saruki et al. 2004) due to excessive vegetation foraging by sika deer. Since then, the forest floor at the study site has been maintained without any understory vegetation. The air and soil temperatures (5 cm depth) of the study site were measured using a temperature logger (TR-51i, T&D Corporation, Matsumoto, Japan), with the mean air and soil temperatures being 8.2 °C and 7.8 °C from

November 2020 to November 2021, respectively (Fig. S4-1). The data showed the soil temperature was often lower than 0 °C during the winter (Fig. S4-1), and freeze–thaw processes were also observed.

By August 2020, the study trees were defined as mature beech trees growing on the ridgeline to the summit of Mt. Sanpo without trunk breakage due to lightning strikes or strong winds. We found a total of 12 beech trees satisfying these criteria. These beeches were present within an area of 250 m × 150 m on slopes ranging from 12° to 45° (Table 4-1, Fig. 4-1). Diameter at breast height (DBH, cm) and tree height (m) of study trees measured in June 2021 were 64.9 ± 17.8 cm and 15.4 ± 1.9 m, respectively. None of the study trees showed any sign of pests or pathogens, such as mass attacks by the beech sawfly, *Fagineura crenativora*.

Table 4-1. Information of slope angle (°), diameter at breast height (DBH, cm), tree height (m), number of points with exposed root height (ERH, cm) >0 cm (Number of ERH), mean ERH, and maximum ERH of beech trees.

Tree numb er	Slope angle	Tree age ^a	DB H	Tree height	Num. of ERH	Mean ERH	Max. ERH	Root & soil ^b
1	21	160	77.7	18.0	6	0.33	10	×
2	32	84	46.9	18.3	4	0.36	22	×
3	45	84	72.9	17.2	9	0.80	27	
4	25	144	44.4	13.3	12	0.93	18	
5	20	114	52.3	15.7	11	1.64	21	
6	18	215	71.9	16.0	17	1.93	22	
7	44	124	59.6	13.4	14	2.49	20	
8	27	243	67.5	13.2	17	2.86	30	×
9	23	141	46.4	16.9	21	3.85	19	
10	40	169	105.9	14.1	23	5.88	39	×
11	41	138	77.6	14.3	23	6.56	51	×
12	12	188	55.4	14.9	37	6.61	31	×

Superscript a: tree age was detected by tree-ring numbers.

Superscript b: trees with “×” were used to the measure fine root biomass, fine root production, litter amount, soil C/N ratio, soil nitrogen concentration, specific root length, and average diameter of fine roots.

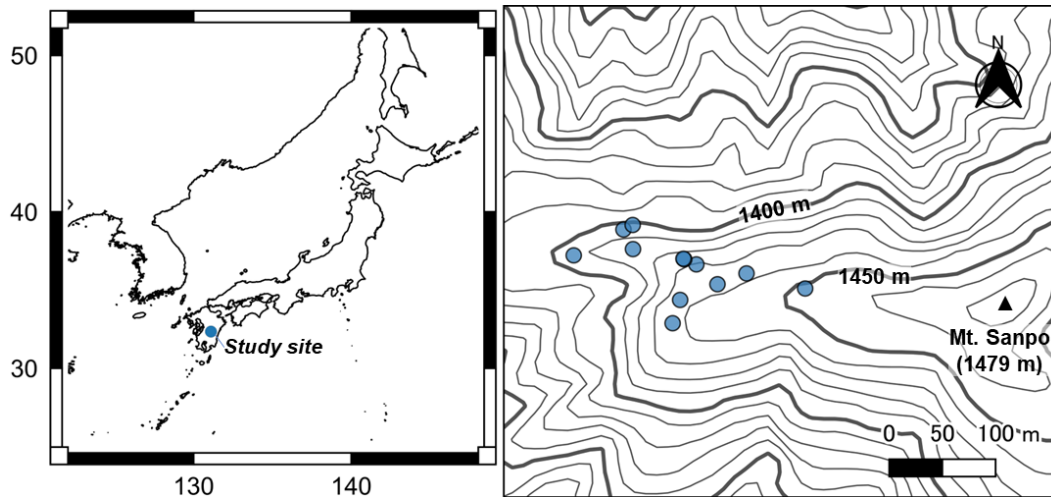


Fig. 4-1. Location of beech trees (*Fagus crenata*) in this study at Mt. Sanpo. The blue dots indicate the positions of the study trees. The thin and thick gray lines indicate contour intervals of 10 m and 50 m, respectively. Contour intervals were obtained from the Geospatial Information Authority of Japan.



Fig. 4-2. Photograph of the study site (a), example of exposed roots (b), and measurement point of exposed roots height (ERH, c). Photograph (a, b) were taken in December 2021. The black arrow lines in panel c indicate the horizontal line, and gray dots indicate the measurement points of ERH.

4.2.2. Exposed root height

In this study, ERH (cm) was defined as the vertical length from the top of the exposed root to the soil surface (Pelfini and Santilli 2006) and used as an index of cumulative soil erosion (Bodoque et al. 2005). The exposed roots were defined as having a diameter of >1 cm and a portion or the whole root exposed above the ground by >1 cm (Fig. 4-2b).

The ERH of each study tree was measured on April 21, 2021. Eight horizontal lines of 500 cm were set at 45° intervals from the top of the slope (0°), centered on the trunk of the study tree (Fig. 4-2c). On each horizontal line, measurement points were set at every 50 cm from the

trunk surface, totaling 80 points per tree. An auxiliary line of 50 cm was orthogonally set to the horizontal line at each measurement point. The highest vertical height of the exposed roots within the auxiliary line was recorded as ERH (cm). The ERH at the measurement points without exposed roots was recorded as 0 cm.

4.2.3. Tree growth

4.2.3.1. Leaf production

Leaf production was evaluated by collecting litter fall in two defoliation periods (October–November 2020 and September–December 2021) using a litter fall trap (0.5 m² in area, 1 m in height). Two litterfall traps were placed under the canopy on the right and left sides of the slope, 1.5 m away from the trunk (24 traps in total). Beech leaves were sorted from the collected litter and dried at a constant temperature of 70 °C for 48 h in a drying oven (DKN812, Yamato Scientific, Japan). Subsequently, the dry weight of the leaves was measured and divided by the trap area to obtain the leaf production (g m⁻² yr⁻¹). Note that no fallen beech branches were captured during sampling.

4.2.3.2. Stem growth

Stem growth was evaluated using tree-ring width records. Two wood cores (diameter: 5.15 mm) were collected from each study tree using an increment borer (10–100, Haglöf Sweden AB, Langsle, Sweden). Wood core samples were extracted at 1.3 m height from the ground on the right and left sides of the slope (24 cores in total) on March 15, 2021. Wood cores were then air dried and sanded using a disk grinder (DGV-105, TAKAGI, Niigata, Japan) and #80–#2000 sandpaper. A flat head scanner (Epson Perfection V700 Photo, SEIKO EPSON, Tokyo, Japan) was used to image the wood cores at 4800 d.p.i. (minimum pixel size = 0.016 mm). The number of annual rings and their widths were recorded using the WinDENDRO 2008 software (Regent Instruments Inc., QC, Canada). The formation year of the outermost ring of each core was assumed to be 2020. Ring widths of the same individual trees were visually cross-dated.

Time-series data for annual ring width were converted to the basal area (BA, cm²), BAI (cm² yr⁻¹), and relative growth rate (RGR, cm² cm⁻² yr⁻¹) (Battaglia et al. 2009; Silva et al. 2010) as follows:

$$BA_n = \pi R_n^2 \quad (\text{Eq. 4-1}),$$

$$BAI_n = BA_n - BA_{n-1} \quad (\text{Eq. 4-2}),$$

$$RGR_n = \ln(BAI_n) - \ln(BAI_{n-1}) \quad (\text{Eq. 4-3}),$$

where R is the radius at 1.3 m height and subscript n is the year of tree-ring formation. To reduce the effect of the potential increase in stem growth at the juvenile age (Sendall et al. 2016) on the temporal growth analysis, data from 1960–2020, when the age of all study trees was at least 20 years, were used (see section 4.2.6.3.).

4.2.3.3. Fine root biomass and production

Fine root biomass and production were measured in six study trees (Table 4-1). On November 2, 2020, we sampled soil cores with a 5-cm diameter and 30-cm depth at four points: upper, lower, left, and right sides of the slope, 1.5 m apart from each trunk (four points per tree, 24 points in total). Living fine roots (≤ 2 mm diameter) were separated from the soil cores, and their dry weights were measured after drying at 70 °C for 48 h. The dry weights were divided by the area of the soil cores to obtain the fine root biomass (g m^{-2}).

Fine root production was estimated using the ingrowth core method (Vogt and Persson 1991; Katayama et al. 2019; Shimono et al. 2022). On November 2, 2020, we installed ingrowth core bags (5 cm in diameter, 30 cm in depth, and 4 mm in mesh size) in vacated soil holes by measuring fine root biomass (four points per tree, 24 points in total). The ingrowth core bags were filled with soil sieved through a 4-mm mesh. We sampled the core bags after one year of *in situ* incubation and then collected fine roots from the core bag. Fine roots were dried at 70 °C for 48 h. Finally, the dry weight of fine roots was measured and divided by the area of core bags and the incubation period (yr) to obtain the fine root production ($\text{g m}^{-2} \text{yr}^{-1}$).

4.2.4. Soil properties

To evaluate soil properties, we measured soil volumetric water content (SVWC), soil N concentration, soil C/N ratio, and litter amount on the soil surface (hereafter litter amount). SVWC was measured four times between April and November 2021 at four points per tree. Measurements were conducted using a handheld SVWC sensor (ML3 Theta Probe, Delta-T Devices, Burwell, UK) at a 5-cm depth. Soil N concentration ($\text{g g}^{-1} \text{N}$) and soil C/N ratio were measured using soils collected for fine root biomass measurements and a CN analyzer (EA1112, Thermo Finnigan, MA, USA). The litter amount was sampled at an area of $0.2 \text{ m} \times 0.2 \text{ m}$ (0.04 m^2) around the point where soil cores were collected (four points per tree, 24 points in total) on November 2, 2020. The sampled litter was dried at 70 °C for 48 h. Dry weight was measured and divided by sampling area (g m^{-2}). Since surface litter is dammed around exposed roots (Han et al., 2023), litter amount sampling around the exposed roots was avoided in this study.

4.2.5. Beech physiological conditions

4.2.5.1. Functional traits of leaves and fine roots

Leaf mass per area (LMA, g m^{-2}), specific root length (SRL, m g^{-1}), and average root diameter (mm) were measured as proxies for water and/or N limitation (Weigelt et al. 2021). LMA was measured on June 10, 2021. Five shoots with sun leaves were randomly collected from each tree at 10–15-m height. Five intact mature leaves, without any signs of damage from insects or diseases, were collected from each shoot (25 leaves per tree). Leaves were imaged using a flat head scanner at 300 d.p.i., and the total leaf area was measured using LIA for Win32 (Yamamoto 2003). After scanning, leaves were dried at 70 °C for 48 h and weighed. The total leaf area was divided by the dry leaf mass to calculate LMA.

The SRL and root diameter were measured using fine roots sampled for fine root biomass measurement and a flat head scanner (see 4.2.3.3). Fine roots were imaged at 300 d.p.i., and the total root length and average diameter were measured using WinRHIZO pro 2013 software (Regent Instruments Inc., QC, Canada). The total root length was then divided by the fine root biomass to calculate SRL.

4.2.5.2. Intrinsic water use efficiency

We measured the iWUE ($\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$) obtained from the $^{13}\text{C}/^{12}\text{C}$ isotope ratio in stem wood (McCarroll and Loader 2004; Wieser et al. 2018). On June 5, 2021, two wood cores were collected from each study tree in addition to stem growth measurements (see 4.2.3.2.). Annual rings from 1961–2020 were cut at 5-year intervals using a stereomicroscope (Leica M205 C, Leica Microsystems, Wetzlar, Germany) and a microtome blade (S35, Feather safety razor, Osaka, Japan). Wood samples were homogenized and milled using a mixer mill (MM400, Retsch, Haan, Germany). A subsample (0.2–0.3 mg) of each wood sample was weighed on a balance (XP2U, Mettler Toledo Japan, Tokyo, Japan) and placed in a tin capsule for isotopic analysis. An isotope ratio mass spectrometer (Delta V, Thermo Fisher Scientific, Bremen, Germany) was used to measure the $^{13}\text{C}/^{12}\text{C}$ ratio of the samples relative to Vienna Pee-Dee Belemnite (V-PDB) standards:

$$\delta^{13}\text{C} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

(Eq. 4-4),

where $\delta^{13}\text{C}$ is the relative $^{13}\text{C}/^{12}\text{C}$ ratio of the samples to V-PDB, and R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the wood sample and V-PDB standards, respectively.

The iWUE, which is the ratio of photosynthetic rate (A) to stomatal conductance to water vapor (g_s), was calculated from the obtained $\delta^{13}\text{C}$ data (Farquhar and Richards 1984):

$$\text{iWUE} = \frac{A}{g_s} = \frac{C_a}{1.6} \times \frac{b - \Delta}{b - a}$$

(Eq. 4-5),

$$\Delta = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}}{1 + (\delta^{13}\text{C}_{\text{plant}} \times 10^{-3})}$$

(Eq. 4-6),

where A is the net photosynthetic rate, g_s is the stomatal conductance to water vapor, C_a is the atmospheric CO_2 concentration (ppm), a is the isotopic fraction of CO_2 through the stomata (4.4‰; Farquhar and Richards, 1984), b is the isotopic fraction of ribulose 1,5-bisphosphate in the leaf carboxylase/oxygenase (Rubisco) and other enzymes (27‰; Farquhar and Richards, 1984), $\delta^{13}\text{C}_{\text{air}}$ is $\delta^{13}\text{C}$ of atmospheric CO_2 , and $\delta^{13}\text{C}_{\text{plant}}$ is $\delta^{13}\text{C}$ of wood samples. The values of C_a and $\delta^{13}\text{C}_{\text{air}}$ from 1961 to 2003 were obtained from McCarroll and Loader (2004). The values of C_a and $\delta^{13}\text{C}_{\text{air}}$ from 2004 to 2014 were obtained from Mauna Loa (Hawaii) records (ESRL Global Monitoring Laboratory 2021). As the data of McCarroll and Loader (2004) and the Mauna Loa records differ in measurement points and methods, the Mauna Loa data were converted based on the data of McCarroll and Loader (2004). The conversion equation was created using data for both measurement years available (1969–2003 for C_a and 1990–2003 for $\delta^{13}\text{C}_{\text{air}}$, Table S4-1, Fig. S4-2).

4.2.5.3. Nitrogen use efficiency

We measured the leaf N concentration using a CN analyzer to examine the response of the study trees at the individual leaf scale to N limitation. Green leaves used for LMA measurements (see 4.2.5.1) and fallen leaves used for leaf production measurements in 2021 (see 4.2.3.1.) were used as analysis samples. The NUE ($\text{g g}^{-1} \text{N}$) of each study tree was determined using the N concentration of the fallen leaves (N_i , g N g^{-1}):

$$NUE = \frac{1}{N_l}$$

(Eq. 4-7).

For the individual leaf scale, NUE can be used as an index of the amount of assimilation per N uptake (Vitousek 1982; Yasumura et al. 2002). The N resorption efficiency (NRE, %) was also examined (Tateno and Takeda 2010):

$$NRE = \frac{(N_g - N_l)}{N_l} \times 100$$

(Eq. 4-8),

where N_g is the N concentration of fallen leaves (g N g^{-1}).

4.2.6. Indices and statistics

4.2.6.1. Exposed root height index

We calculated the representative value of ERH, i.e., the number of measurement points of $ERH > 0$ cm (number of ERH), mean ERH, and maximum ERH. The number of ERH was expressed as an indicator of the areal extent of erosion. The mean ERH was expressed as the average degree of erosion. The maximum ERH was expressed as the potential degree of erosion (Bodoque et al. 2005). The ERH indices were used as an explanatory variable or fixed effect in a linear regression model (LM) and a linear mixed-effects model (LMM).

4.2.6.2. Relationships between root exposure and current beech growth

To confirm the relationship between ERH and beech growth, the effects of the ERH index on leaf production, RGR of stem growth in 2020, fine root biomass, and fine root production were evaluated using the LM. For leaf production, the LMM was used with the measurement year as a random effect because it was measured in 2020 and 2021.

4.2.6.3. Long-term trends of stem growth

To determine the timing of changes in tree growth, the annual BAI trend from 1960 to 2020 was evaluated. We conducted a segmented time-series regression analysis of the BAI. The “*segmented*” package in R software was employed to detect the break-point (calendar yr, i.e., the changing point of temporal trend in BAI) and the temporal trend before and after the break-point (Muggeo 2008):

$$BAI_n = \begin{cases} \beta_0 + \beta_1 T, & T < \psi \\ \beta_0 + \beta_1 T + \beta_2 (T - \psi), & T \geq \psi \end{cases} \quad (\text{Eq. 4-9}),$$

where T is the calendar year (yr), ψ is the year of the break-point (yr), and β is the parameter. In this equation, β_0 , β_1 , and β_2 are considered as intercepts, slope of the BAI trend before the break-point, and difference in the BAI trend before and after the break-point, respectively. Parameters β , T , and ψ were determined using the lowest residual sum of squares of the model (Muggeo 2008). The relationship between the slope of the BAI trend before (i.e., β_1) and after the break-point (i.e., $\beta_1 + \beta_2$) and the ERH index was tested using LM.

4.2.6.4. Effects of water and N limitation through soil erosion on tree growth

The following two analyses were performed using soil properties and beech physiological condition data to assess possible mechanisms for tree growth reduction. First, the effects of the ERH index on soil properties such as SVWC, litter amount, soil N concentration, and soil C/N ratio were evaluated using the LM. For SVWC, the LMM was used with the measurement date as a random effect. The effects of the ERH index on beech physiological conditions (i.e., LMA, SRL, fine root diameter, iWUE, green leaf N concentration, NUE, and NRE) were also evaluated using the LM. The iWUE was examined separately before and after the break-point of the BAI. Second, to assess the effects of water and N limitations on beech growth, the relationships between BAI and iWUE were examined separately before and after the break-point using LM. The objective variable was BAI, and the explainable variable was iWUE. In addition, the relationship between NUE and NRE to leaf production in 2021 was examined using LM. The objective variable was leaf production in 2021, and the explainable variables were NUE or NRE.

The adjusted coefficient of determination (adjusted R^2) and coefficient of determination explained by fixed effects (marginal R^2) were evaluated as the model fit of LM and LMM (Nakagawa and Schielzeth 2013), respectively. The threshold for statistical significance was set at $p < 0.05$. In addition, due to the small sample size, we assumed that results with $p < 0.10$ had marginally significant one. In this study, LM and LMM were conducted using each of the three ERH indices (i.e., number of ERH, mean ERH, and maximum ERH) as explanatory variables or fixed effects. To control the familywise error rate, which is the probability of making at least one type I error (rejecting the null hypothesis when it is true) across three ERH indices, Dunn–Šidák-adjusted p -values (hereafter, adjusted p -value) were calculated for each objective variable in addition to the normal p -value. All statistical analyses were performed using R software ver. 4.0 (R Core Team 2024).

4.3. Results

4.3.1. Relationships between root exposure and beech growth

The value of ERH varied among individuals. The number of ERH, mean ERH, and maximum ERH per individual ranged from 4–37 points, 0.33–6.61 cm, and 10–51 cm, respectively. The mean value and standard deviation (SD) of the number of ERH, mean ERH, and maximum ERH for each study tree were 16.2 ± 9.1 points, 2.9 ± 2.4 cm, and 25.8 ± 10.9 cm, respectively (Table 4-1).

The ERH indices were negatively correlated with leaf production and RGR, whereas they did not correlate with fine root biomass and production (Table 4-2, Fig. 4-3). The mean value and SD of leaf production were 73.3 ± 39.1 g m⁻² yr⁻¹ in 2020 and 102.9 ± 50.1 g m⁻² yr⁻¹ in 2021. Leaf production was negatively related to the number of ERH and mean ERH (number of ERH, marginal $R^2 = 0.40$, $p = 0.003$, adjusted $p = 0.009$; mean ERH, marginal $R^2 = 0.37$, $p = 0.004$, adjusted $p = 0.012$, Fig. 4-3a). In addition, RGR in 2020 (0.0079 ± 0.0055 cm² cm⁻² yr⁻¹) was negatively related to the number of ERH (adjusted $R^2 = 0.39$, $p = 0.017$, adjusted $p = 0.049$) and marginally negatively related to mean ERH (adjusted $R^2 = 0.37$, $p = 0.022$, adjusted $p = 0.065$, Fig. 4-3b). In contrast, all ERH indices were not related to fine root biomass (155.2 ± 67.2 g m⁻²) and fine root production (175.8 ± 109.8 g m⁻², Fig. 4-3c).

Table 4-2. Effects of three exposed root height (ERH) indices (i.e., Number of ERH, Mean ERH, and Maximum ERH) on beech production, beech physiological conditions, and soil properties. The value in the R^2 column shows the results of individual ERH index and represents adjusted R^2 for the linear model (LM) and marginal R^2 for the linear mixed-effects model (LMM). Subscripts plus and minus in the R^2 column indicate a significant positive or negative relationship between the ERH index and the other variables, respectively. The p column values are original p -values, and Dunn–Šidák-adjusted p -values are shown in parentheses. Results with original $p < 0.05$ are shown in boldface. Results with original $p < 0.05$ but Dunn–Šidák-adjusted p -value > 0.05 are shown in italics.

Variables	Number of ERH		Mean ERH		Maximum ERH	
	R^2	p	R^2	p	R^2	p
Beech growth						
Leaf production ^a	0.40⁻	0.003 (0.009)	0.37⁻	0.004 (0.012)	0.18⁻	0.039 (0.112)
RGR in 2020	0.39⁻	0.017 (0.049)	0.37⁻	0.022 (0.065)	0.15	0.118 (0.314)
Fine root biomass	-0.25	0.932 (1.000)	-0.22	0.775 (0.989)	-0.17	0.618 (0.944)
Fine root production	-0.25	0.919 (0.999)	-0.24	0.894 (0.999)	-0.25	0.917 (0.999)
Slope of BAI before BP	-0.09	0.788 (0.990)	-0.05	0.499 (0.874)	0.07	0.205 (0.498)
Slope of BAI after BP	0.73⁻	<0.001 (<0.001)	0.71⁻	< 0.001 (<0.001)	0.31⁻	0.033 (0.099)
Beech physiological condition						
LMA	-0.03	0.435 (0.820)	-0.09	0.820 (0.994)	-0.04	0.457 (0.84)
SRL	0.01	0.359 (0.737)	-0.24	0.837 (0.996)	-0.25	0.913 (0.999)
Fine root diameter	0.08	0.298 (0.654)	-0.25	0.990 (1.000)	-0.13	0.543 (0.905)
Green leaf N concentration	-0.09	0.808 (0.993)	-0.04	0.459 (0.842)	0.11	0.156 (0.399)
iWUE before BP	-0.04	0.475 (0.855)	-0.03	0.443 (0.827)	-0.10	0.965 (1.000)
iWUE after BP	-0.09	0.745 (0.983)	-0.10	0.926 (1.000)	-0.10	0.981 (1.000)
NUE	0.13	0.132 (0.346)	0.24	0.061 (0.172)	0.28⁻	0.045 (0.129)
NRE	0.08	0.197 (0.482)	0.30⁺	0.039 (0.112)	0.49⁺	0.006 (0.018)

Continued to next page

Table 4-2. (Continued)

Variables	Number of ERH		Mean ERH		Maximum ERH	
	R^2	p	R^2	p	R^2	p
Soil properties						
SVWC ^a	0.09 ⁺	0.047 (0.134)	0.15 ⁺	0.033 (0.096)	0.14	0.09 (0.246)
Litter amount	-0.25	0.944 (1.000)	-0.23	0.831 (0.995)	-0.14	0.567 (0.919)
Soil N concentration	-0.25	0.973 (1.000)	-0.19	0.666 (0.963)	-0.20	0.717 (0.977)
Soil C/N ratio	-0.23	0.821 (0.994)	-0.15	0.588 (0.930)	0.04	0.331 (0.701)

Abbreviations: ERH, exposed root height; RGR, relative growth rate for stem growth; BAI, basal area increment; LMA, leaf mass per area; SRL, specific root length; iWUE, intrinsic water use efficiency; N, nitrogen; NUE, nitrogen use efficiency; NRE, nitrogen reportion efficiency; SVWC, soil volumetric water content; Soil C/N ratio, soil carbon/nitrogen concentration ratio.

Superscript a: Regression analysis of these variables was performed using the LMM.

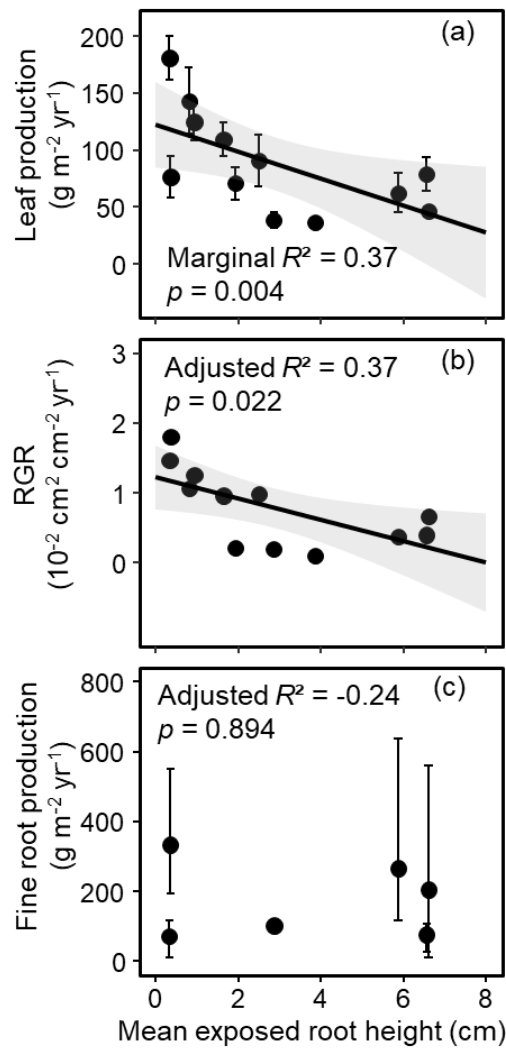


Fig. 4-3. Relationships between mean exposed root height (ERH) and both leaf production (a), relative growth rate (RGR) of stem growth in 2020 (b), and fine root production in 2021 (c). The circle indicates mean values, and error bars indicate maximum and minimum values. The solid line indicates the significant regression line, and the gray area indicates the 95% confidence intervals.

4.3.2. Long-term trends of stem growth

Segmented regression analysis revealed that the BAI of the study trees showed decreasing trends after its own break-point (Fig. 4-4), except for individuals No. 3 and No. 7 (Table 4-1). The mean value and SD of break-points for individuals with a negative BAI trend after the break-point was 1997.6 ± 9.0 yr (Fig. 4-4). All ERH indices were not related to the slope of the BAI trend before the break-point, whereas these were negatively related to the BAI trend after the break-point (e.g., relationships with mean ERH: $p = 0.499$ before break-point, $p < 0.001$ after break-point, Table 4-2, Fig. 4-5).

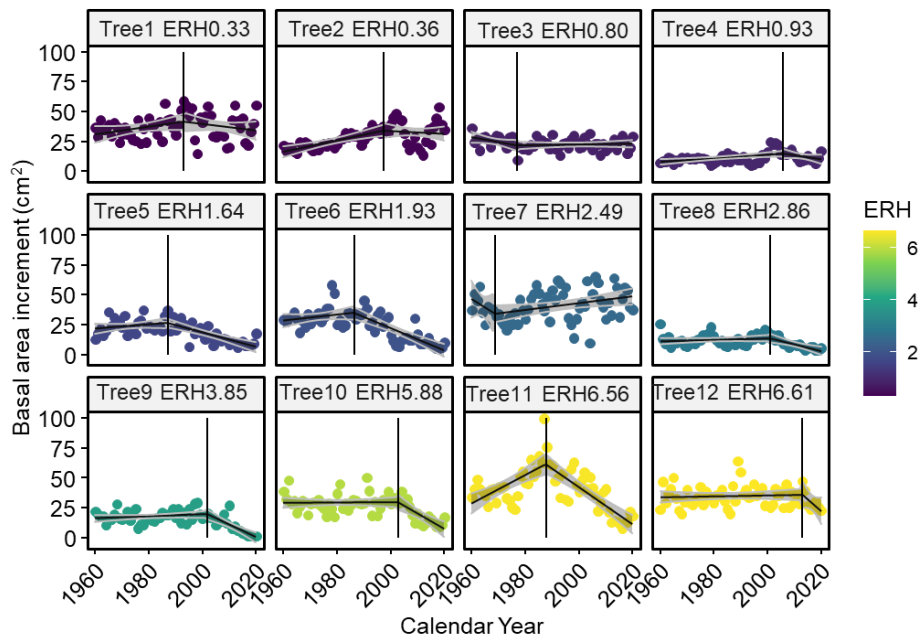


Fig. 4-4. Temporal trend of basal area increment (BAI). Each graph shows the results for each tree sorted by mean exposed root height (ERH, cm). The numbers of each tree correspond to those in Table 4-1. The circle indicates the measured value. The solid black line indicates the results of the segmented regression line, and the gray area indicates the 95% confidence intervals. The black vertical lines indicate the year of break-points.

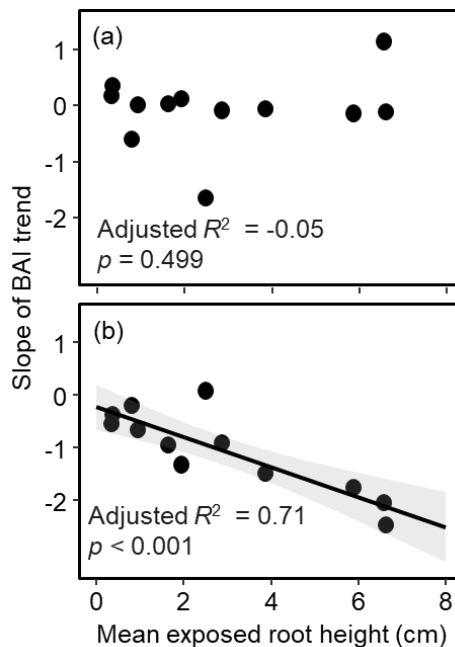


Fig. 4-5. Relationship between mean exposed root height and slope of BAI trend in periods before break-point of BAI (a) and in periods after break-point of BAI (b). The circle indicates the measured value. The solid line indicates the significant regression line, and the gray area indicates the 95% confidence intervals.

4.3.3. Potential effects of water and nitrogen limitation

4.3.3.1. Soil properties and beech physiological conditions in relation to root exposure

SVWC was marginally positively related to the number of ERH and mean ERH (Table 4-2). Soil N concentration ($1.3 \pm 0.1\%$), soil C/N ratio (11.3 ± 0.7), and litter amount ($97.9 \pm 47.9 \text{ g m}^{-2}$) were not related to all ERH indices (Table 4-2). The LMA ($95.9 \pm 12.5 \text{ g m}^{-2}$), SRL ($16.9 \pm 6.7 \text{ m g}^{-1}$), and average diameter of fine roots ($0.34 \pm 0.06 \text{ mm}$) were not related among all ERH indices (Table 4-2).

The 5-year-interval trends of iWUE showed slightly increasing trends from before break-points ($65.9 \pm 5.0 \mu\text{mol mol}^{-1}$) to after break-points ($69.6 \pm 10.9 \mu\text{mol mol}^{-1}$, Table S4-1, Fig. 4-6). Both iWUE before and after break-points did not relate to any ERH indices (Table 4-2).

The mean value and SD of green leaf N concentrations, NUE, and NRE were $3.0 \pm 0.2\%$, $67.0 \pm 6.3 \text{ g g}^{-1} \text{ N}$, and $49.4 \pm 5.9\%$, respectively. No relationships existed between the green leaf N concentration and any ERH indices (Table 4-2). NUE was marginally negatively correlated with maximum ERH (adjusted $R^2 = 0.28$, $p = 0.045$, adjusted $p = 0.129$). NRE was positively related to maximum ERH (adjusted $R^2 = 0.49$, $p = 0.006$, adjusted $p = 0.018$) and marginally negatively related to mean ERH (adjusted $R^2 = 0.30$, $p = 0.039$, adjusted $p = 0.112$).

4.3.3.2. Relationships between beech physiological conditions and growth

We found no significant relationship between iWUE and BAI before the break-point (adjusted $R^2 = 0.10$, $p = 0.168$, Fig. 4-7a), whereas a negative relationship was observed after the break-point (adjusted $R^2 = 0.26$, $p = 0.049$, Fig. 4-7b). There were positive relationships between leaf production in 2021 and NUE (adjusted $R^2 = 0.50$, $p = 0.006$, Fig. S4-3a) and no relationships between leaf production in 2021 and NRE (adjusted $R^2 = 0.23$, $p = 0.068$, Fig. S4-3b).

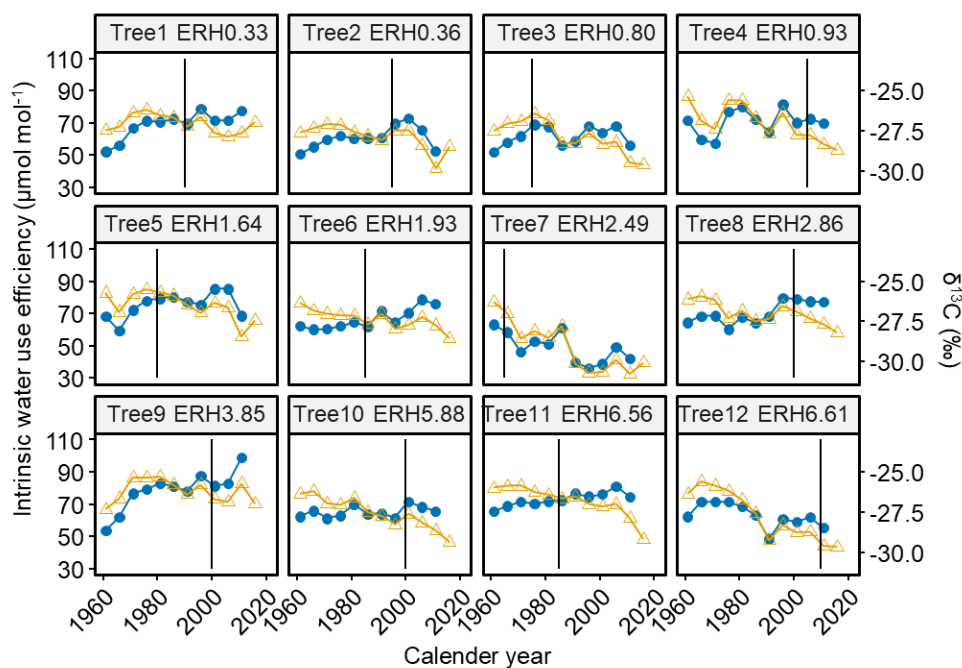


Fig. 4-6. Temporal trend of $\delta^{13}\text{C}$ and intrinsic water use efficiency (iWUE). Each graph shows the results for each tree sorted by mean exposed root height (ERH, cm). The numbers of each tree correspond to those in Table 4-1. The circle with a solid blue line indicates the results of iWUE. The open triangle with a solid orange line indicates the results of $\delta^{13}\text{C}$. $\delta^{13}\text{C}$ and iWUE were measured at 5-year intervals, and points were plotted in the starting year of each measurement interval. Black vertical lines indicate the year of break-points of basal area increment (BAI) adjusted at 5-year intervals.

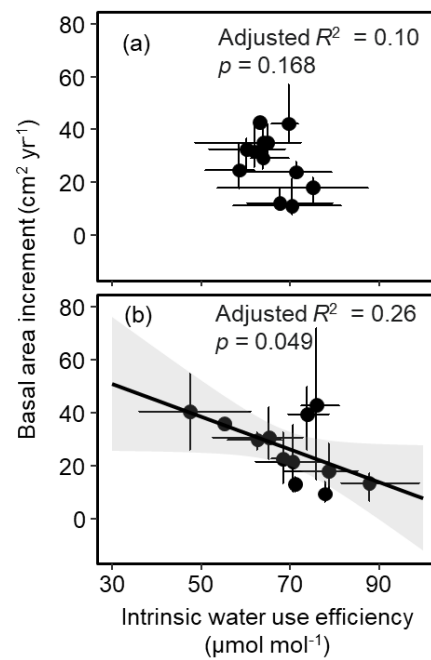


Fig. 4-7. Relationships between intrinsic water use efficiency (iWUE) and basal area increment (BAI) in periods before break-point of BAI (a) and periods after the break-point of BAI (b). The circle indicates mean values, and error bars indicate maximum and minimum values. The solid line indicates a significant regression line, and the gray area indicates the 95% confidence intervals.

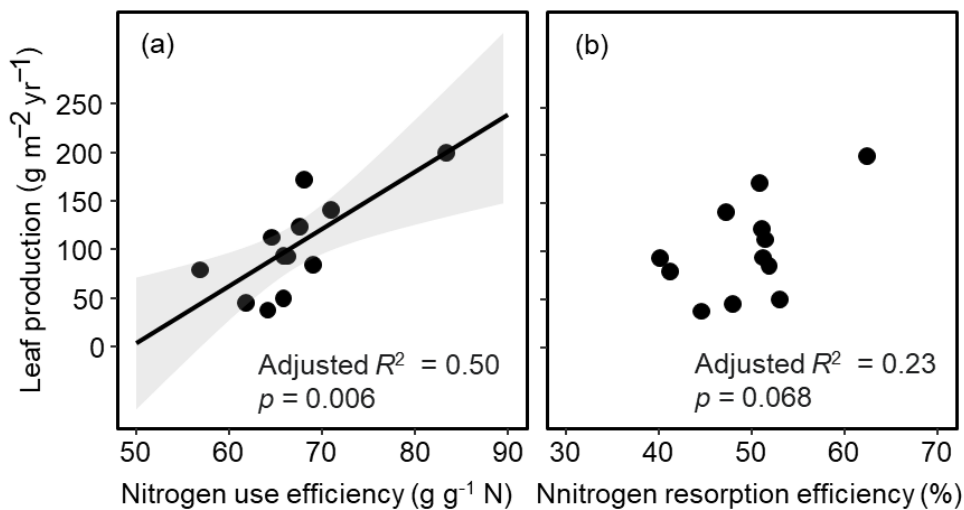


Fig. 4-8. Relationships between leaf production in 2021 and both of nitrogen use efficiency (a) and nitrogen resorption efficiency (b). Circles indicate measured values. The solid line indicates the significant regression lines and the gray areas indicates the 95% confidence intervals.

4.4. Discussions

4.4.1. Root exposure due to understory degradation

We found considerable root exposure up to 51 cm based on maximum ERH (Table 4-1). Mean value of maximum ERH (25.8 cm) in the present study was 2.7 times higher than that in forests affected by slope failure (9.4 ± 6.1 cm in Hupp and Carey, 1990), 2.8–6.8 times higher than that in forests impacted by trail running (3.8–7.8 cm in Bodoque et al., 2005; 7.4–9.3 cm in Pelfini and Santilli, 2006), and 9.9–13.6 times higher than that in grasslands experiencing high sheep grazing pressure (1.9–2.6 cm in Chartier et al., 2008) (Table S4-2). Although there were differences in target tree species, geology, and climate between the current and previous study sites, the understory vegetation degradation in forest ecosystems by sika deer herbivory was found to detach topsoil as much as or more than slope failure, trail running, and sheep grazing.

4.4.2. Relationships between soil erosion and beech growth reduction

At the study site, beech trees with a higher ERH index had a lower amount of leaf production and a lower value of RGR (Table 4-2, Fig. 4-3a, b). In contrast, fine root production was not related to the ERH index (Fig. 4-3c). These results suggest that individuals with a high ERH index have lower above-ground growth than those with a low ERH index; thus, the first hypothesis was confirmed. The impact of soil erosion on plant productivity has long been discussed, but most of the literature has focused on agricultural land (National Soil Erosion-Soil Productivity Research Planning Committee 1981; Jiao et al. 2009; Quinton et al. 2010). The present study revealed that soil erosion caused by understory degradation also caused mature tree growth reduction in forest ecosystems, which was the first attempt to thoroughly demonstrate the influence of soil erosion at the individual tree level.

4.4.3. Period of reduced beech growth

Segmented regression analysis revealed that the break-point of BAI occurred around 1998 (1997.6 ± 9.0), and BAI after the break-point showed decreasing trends (Fig. 4-4). In the study area, an increase in deer population size has been observed since the 1980s, and understory vegetation had mostly disappeared by 2003 (Saruki et al. 2004). The break-point of the study trees was within the period of understory vegetation degradation in the study area. In addition,

the decreasing BAI trends after the break-points were negatively related to the ERH index (Table 4-2, Fig. 4-5). These results indicate that beech growth reduction through soil erosion has occurred since the understory vegetation degradation and hence supports the second hypothesis. Note that the present study only used the ERH to assess the cumulative degree of erosion around a tree. Therefore, the start date of root exposure for individual trees remains unclear. This limitation could be addressed by confirming the coincidence between the timing of changes in tissue structure associated with root exposure on a yearly basis (Gärtner 2007) and the timing of BAI reduction in the present study.

4.4.4. Factors causing the beech growth reduction

The iWUE and BAI were not related before the break-point and were negatively related after the break-point (Fig. 4-7). As iWUE indicates plant water stress, i.e., higher iWUE indicates a higher level of water limitation (Zadworny et al. 2019). These results suggest that beech growth at the study site may have been reduced due to water limitation, supporting the third hypothesis. The increase of iWUE can be explained by root exposure due to soil detachment. Root exposure may lead to the death of fine roots due to drying and freezing (Weih and Karlsson 2002; Cleavitt et al. 2008) and hydraulic failure in xylem conduction of coarse roots (Pittermann and Sperry 2003; Mayr et al. 2007; Arbellay et al. 2012). Freezing death of fine roots and winter embolism is likely to occur in this study area because the soil temperature is often lower than 0 °C (Fig. S4-1), and freeze-thaw processes were observed in the winter season. Generally, water-limited trees are expected to respond to reduced water supply by closing individual leaf stomata (Hereş et al. 2014) and reducing leaf production (Vicente-Serrano et al. 2015). Stomatal closure and reduced leaf production lead to reduced photosynthetic rates in individual leaves and whole-tree photosynthesis, thereby reducing tree production (Wieser et al. 2018). Thus, beech growth in our study site is reduced due to water limitation associated with root exposure. Note that we measured iWUE as an integrated indicator of water limitation; however, we did not measure other indicators of water limitation. Future studies should include more accurate investigations of water limitation and beech growth, including the hydraulic conditions of exposed roots.

In addition to root exposure, reduction of SVWC also causes water limitation, i.e., an increase in iWUE. However, the SVWC was not affected by ERH indices at the study site (Table 4-2). Possible reasons for this lack of reduction in SVWC include the effects of

understory degradation and methodological issues. Kawakami et al. (2020) reported that understory degradation did not decrease SVWC in forests near the present study site (approximately 9 km away from the study site, 1180 m above sea level) because of reduced consumption of soil water by understory vegetation. In addition, present study evaluated soil water capacity by only monitoring the SVWC of the surface layer over a short period. The SVWC varies widely within a day, season, and year (Chen et al. 2017; Bai et al. 2019). It is unknown whether water limitation was attributed via soil water availability only through short-term comparisons (Rasheed et al. 2022). For these reasons, the short-term monitoring did not allow us to observe evidence of a decrease in SVWC in the study area.

The NUE and NRE indicate plant N stress; consequently, they are negatively correlated with tree production when N limitation occurs (Yasumura et al. 2002; Tateno and Takeda 2010; Maeda et al. 2018; Shimono et al. 2022). In the present study, the increase in ERH did not decrease soil N concentration at the study site (Table 4-2). Also, neither NUE nor NRE were negatively related with leaf production in the present study (Fig. S4-3). The soil N concentration results were comparable to that of forests near the study site where the understory vegetation is still present (Kawakami et al., 2020). Moreover, NUE in this study ($67.0 \pm 6.3 \text{ g g}^{-1} \text{ N}$) was close to the lower limit of the range ($60\text{--}90 \text{ g g}^{-1} \text{ N}$) observed for beeches growing in cool-temperate deciduous forests with understory vegetation in central Japan (Tateno and Takeda 2010). Therefore, we could not detect the reduction in soil N concentration and response of beeches to N-limited conditions at the individual leaf level at the study site.

Although we found that soil erosion was the factor reducing tree growth, other factors have been reported to reduce tree growth in Japan. Previous studies that reported beech decline in Japan have organized the mechanism of beech decline in mountain forests in Japan as a “multiple-factor theory” (Kohno 2017). According to this theory, beech growth in this study site is reduced via water limitation (i.e., an increase of iWUE) due to multiple factors, including air pollution such as increasing ozone concentration (Yamaguchi et al. 2011), and the impacts of global warming such as rising temperatures and aridity (Matsui et al. 2009). Beech trees with reduced growth might die due to disturbances such as physical shocks from strong winds (Suto et al. 2008) and mass attack by the beech sawfly, *Fagineura crenativora* (Tani et al. 2008). Similarly, increased tree mortality due to a combination of climate change and tree diseases has been reported for European oak (Thomas 2008) and American beech (Stephanson and Ribarik Coe, 2017). Therefore, it can be inferred that root exposure due to soil erosion, combined with

the multiple factors described above, accelerates the decline and death of beech. Furthermore, soil erosion and beech growth reduction shown in this study support the “Erosion positive feedback loop hypothesis” proposed by Flores et al. (2020). They hypothesized that soil erosion after forest fire leads to reduced forest production, reducing litter cover on the forest floor and further increasing soil erosion. At this study site, soil erosion and reduced beech growth may also create a self-reinforcing feedback loop, resulting in further severe soil erosion and ecosystem degradation.

4.4.5. Conclusion

This chapter revealed that forest soil erosion leads to spatially heterogeneous tree growth reduction, reflecting the sporadic nature of soil erosion. Specifically, we identified that the 10–51 cm soil layer was eroded due to understory vegetation degradation based on the maximum ERH. We also found that above-ground growth of beech with higher ERH was suppressed possibly because of the water limitation associated with root exposure following the understory degradation. Spatially heterogeneous tree degradation is speculated to lead to reduced reproduction in the community, including failure of pollination and seed production by degraded trees (Ichie et al. 2013; Burczyk et al. 2019). Community instability will result in a progressive decline in forest ecosystem functions such as C stocks and biodiversity (White 2012). Based on differences in root system distribution and hydraulic properties, the susceptibility of root exposure and vulnerability of tree production to soil erosion may vary among tree species. Thus, future research should investigate variation in root exposure and its effects on the tree production in a variety of tree species as well as the impact of soil erosion on forest ecosystem stability and functions.

4.5. Supplemental materials

Table S4-1. Temporal change of $\delta^{13}\text{C}$ and intrinsic water use efficiency (iWUE)

Period	Atmospheric CO_2 (Mean, ppm) ^a	Atmospheric $\delta^{13}\text{C}$ (Mean, ‰) ^a	$\delta^{13}\text{C}$ of wood (Mean $\pm$ SD, ‰)	iWUE (Mean $\pm$ SD, μmol mol^{-1})
1961–1965	318.78	–7.0	–26.5 $\pm$ 0.8	60.3 $\pm$ 7.0
1966–1970	323.22	–7.1	–26.6 $\pm$ 0.6	61.7 $\pm$ 5.4
1971–1975	328.82	–7.2	–26.6 $\pm$ 0.9	63.9 $\pm$ 8.4
1976–1980	335.24	–7.4	–26.5 $\pm$ 0.8	67.6 $\pm$ 8.1
1981–1985	342.68	–7.5	–26.7 $\pm$ 0.9	69.0 $\pm$ 8.8
1986–1990	350.78	–7.7	–27.2 $\pm$ 0.8	67.0 $\pm$ 8.1
1991–1995	357.72	–7.8	–27.7 $\pm$ 1.1	63.7 $\pm$ 11.7
1996–2000	365.5	–7.9	–27.5 $\pm$ 1.3	68.3 $\pm$ 13.5
2001–2005	373.38	–8.1	–27.7 $\pm$ 1.1	68.8 $\pm$ 12.2
2006–2010	381.94	–8.2	–27.8 $\pm$ 0.9	71.2 $\pm$ 10.2
2011–2015	393.63	–8.3	–28.5 $\pm$ 1.3	66.3 $\pm$ 15.0 ^b
2016–2020			–28.6 $\pm$ 1.1	

Superscript a: atmospheric CO_2 concentration and $\delta^{13}\text{C}$ were obtained from the annual data of McCarroll and Loader (2004) and Mauna Loa (Hawaii) records (ESRL Global Monitoring Laboratory, 2021).

Superscript b: iWUE in this period is calculated from 2011–2014.

Table S4-2. Comparison of maximum exposed root height (Max ERH) between this study and previous studies. Column of driver indicates the factors driving the erosion and the column of duration indicates the periods of time between the occurrence of erosion and the measurement of ERH.

Country	MAT (°C)	MAP (mm)	Slope (°)	Driver	Study tree	Duration (yr)	Max ERH (cm)	Reference
Japan	8.2	2750	12–45	Deer overbrowsing	<i>F. crenata</i>	17–41 ^a	25.8 ± 10.7	This dissertation
USA	N/A	1153	23–38	Slope failure	<i>Q. montana</i>	22–39	9.4 ± 6.1	Hupp and Carey, 1990
Spain	6	1400	23	Human trampling	<i>P. sylvestris</i>	7–101	7.8 ± 2.8	Bodoque et al., 2005
	11.5	450	14		<i>Q. ilex</i>	34–61	3.8 ± 1.7	
Italy	N/A	N/A	N/A	Human trampling	<i>L. decidua</i>	20–25	7.4–9.3 ^b	Pelfini and Santilli, 2006
Argentina	12.5	258	1–5	Sheep grazing	<i>M. pinnatus</i>	8–9	1.9 ± 0.2	Chartier et al., 2009
			2–3			9–10	2.6 ± 0.2	

Abbreviations: MAT, mean annual air temperature; MAP, mean annual precipitation; N/A, not available. Abbreviations of genus of study trees: *F*, *Fagus*; *Q*, *Quercus*; *P*, *Pinus*; *L*, *Larix*; *M*, *Margyricarpus*.

Superscript a: Although the duration of soil erosion in this study is not known, the decline of understory vegetation was observed from around 1980 and almost disappeared in 2004 (Saruki et al., 2004). Based on this, we assumed that soil erosion occurred from 1980 or 2004 to the year of ERH measurement (2021), i.e., 17–41 years.

Superscript b: Pelfini and Santilli (2006) only reports the soil erosion rate (0.37 cm yr⁻¹) which was calculated from ERH and duration time between year of root exposed and measurements of ERH (20–25 years). Thus, we estimated maximum ERH (7.4–9.3 cm) by the multiplying the soil erosion rate and the duration time.

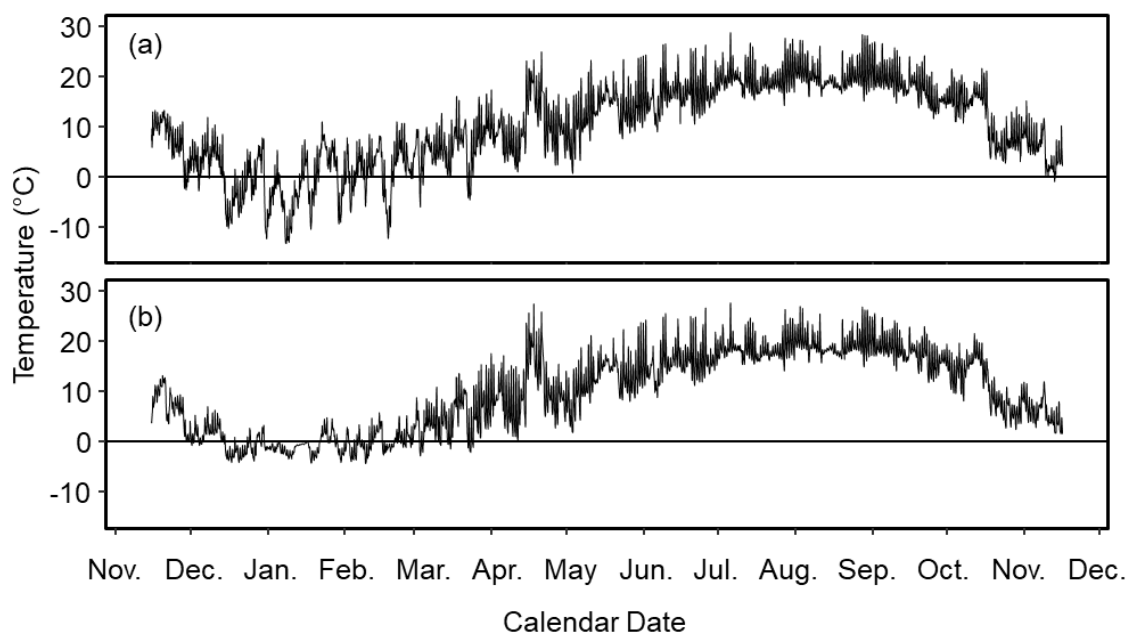


Fig. S4-1. Hourly air temperature (a) and soil temperature at 5 cm depth (b) at the study site. Data were collected from November 15, 2020, to November 15, 2021.

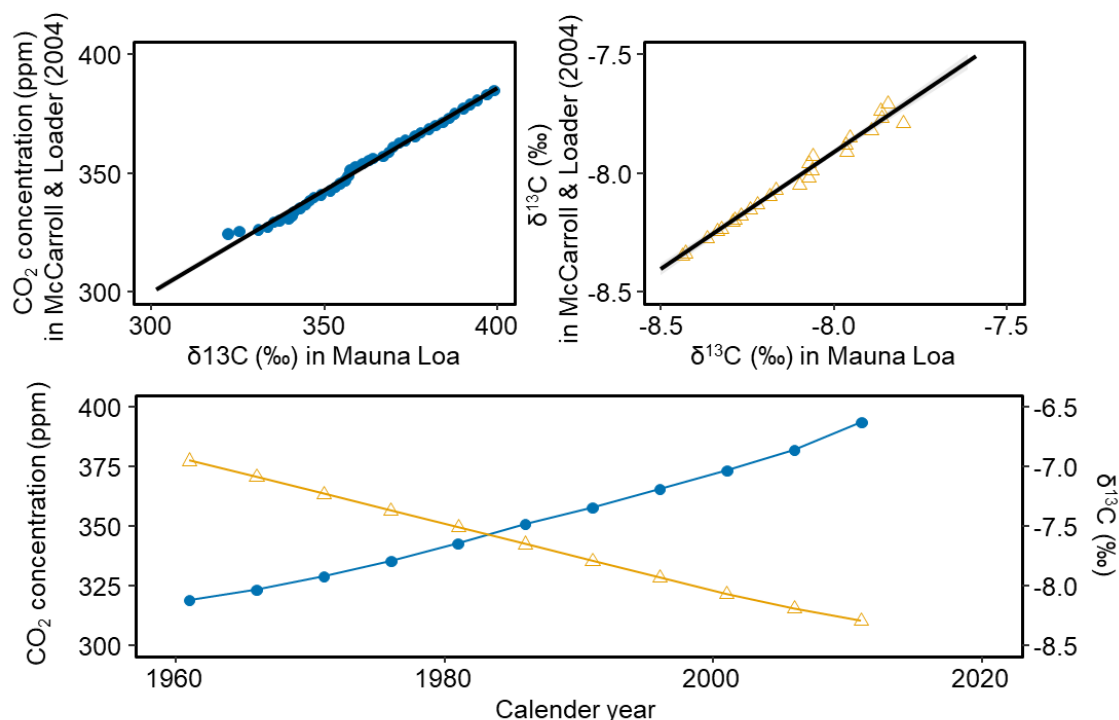


Fig. S4-2 Correlations between atmospheric CO₂ concentration (a) and atmospheric $\delta^{13}\text{C}$ (b) obtained by McCarroll & Loader (2004) and at Mauna Loa records (ESRL Global Monitoring Laboratory, 2022), and the temporal trend of CO₂ concentration and $\delta^{13}\text{C}$ used to calculate the intrinsic water use efficiency (c).

Chapter 5: Degradation in forest carbon sequestration due to deer-induced stand structural alteration

5.1. Introduction

Maintaining forest carbon (C) sequestration (FCS) is a global goal for sustainable forest management (Ontl et al. 2020). The strength of FCS varies with stand structure, including tree species diversity, stem density, and tree height (Ali 2019). Ungulates play a key role in regulating stand dynamics and associated FCS by feeding on understory vegetation (Forbes et al. 2019; Landuyt et al. 2019). However, as shown in chapter 4, prolonged excessive vegetation feeding by ungulates (overbrowsing) leads to loss of understory vegetation (Suzuki 2024). Overbrowsing-induced understory degradation may alter stand dynamics and FCS (Allen et al. 2023; Dobor et al. 2024). Further research examining this possibility is necessary to guide forest management decisions regarding overbrowsing.

FCS can be evaluated by the amount of C stocks and net C absorption (Siry et al. 2005; Fuss et al. 2018). The net C absorption is expressed as net ecosystem C balance (NECB), which is the balance between C uptake through net primary production (NPP), as well as C release through heterotrophic respiration (HR) and other C flux pathways, such as soil C loss by sediment transport (SE). To date, comparative studies of specific C stock components or NECB components between areas inside and outside ungulate-exclosure fences have been the primary approach for determining the impacts of overbrowsing on FCS (Leroux et al. 2020). These findings have shown that overbrowsing leads to decrease understory vegetation biomass (Schreiner et al. 1996; Stark et al. 2000; Kooijman and Smit 2001; Nomiya et al. 2003) and related NPP, e.g., reductions in litterfall (Ramirez et al. 2018; Forbes et al. 2019; Leroux et al. 2020) and fine root production (Ruess et al. 1998). In addition, overbrowsing decreases microbial basal respiration, which can contribute to reduced HR (Stark et al. 2000). As shown in chapter 4, overbrowsing increases the soil erosion rate (Mizuno et al. 2021), meaning an increment of SE. In addition, it has been reported that the reductions in the amount of leaf litter and fine woody debris (FWD) (Kooijman and Smit 2001), as well as slight reductions in soil organic matter (SOM) stocks (Binkley et al. 2003). These partial evidence suggests that overbrowsing may reduce the NECB and hence decrease C stocks in forests. However, it is not easy to synthesize the findings of previous studies because they targeted different ungulate

species, different forest types, climates, and geology. The first step in verifying the above possibility is to comprehensively evaluate FCS within the same forest landscape with fixed ungulate species and environmental conditions.

Previous studies comparing FCS inside and outside the fence have another limitation—they focus primarily on the presence or absence of overbrowsing in forests with the same stand structure. In other words, few studies focus on changes in FCS in response to various stand structural alterations by overbrowsing. Based on chapter 4, the loss of understory vegetation causes overstory tree declines. Overbrowsing promotes the expansion of unpalatable plant species (Tremblay et al. 2006; Forbes et al. 2019) and inhibits tree renewal of palatable species in canopy gaps (Shinoda and Akasaka 2020; Tsujino and Matsui 2022; Ang et al. 2022). The combination of declining overstory trees and hampered forest regenerations has resulted in heterogeneous forest stand structures within the forest landscape (Fig. 5-1a) (Schmitz et al. 2018; Forbes et al. 2019). Literature reviews predict that the overbrowsing-induced FCS degradation will be maximized when overstory trees disappear due to the inhibition of tree renewal and/or replacement with unpalatable plants (Leroux et al., 2020; Ramirez et al., 2018). This prediction implies that overstory-induced FCS degradation may vary with the type of stand structural alterations. Thus, it is necessary to investigate C stocks and NECB in each of the multiple stand structural alterations to examine effective overbrowsing countermeasures within the landscape.

In Kyushu University Shiiba research forest (SRF), overbrowsing has led to the alteration of broadleaf-conifer mixed stands with understory vegetation (presence of understory; PU, Fig. 5-1b) into stands with no understory vegetation (no understory; NU, Fig. 5-1c) (Saruki et al., 2004). Overbrowsing has then promoted the expansion of unpalatable shrub species, Asebi (*Pieris japonica*) in NU with high light availability (Tokumoto and Katayama 2024). This has altered NU into stands dominated by Asebi (shrublands; SR, Fig. 5-1d). Overbrowsing has also altered NU into stands with canopy gap areas (canopy gaps; CG, Fig. 5-1e) due to the failure of palatable tree regeneration following overstory mortality (Shinoda and Akasaka, 2020). This chapter examined how much deer-induced stand structural alterations degrade C stocks, NECB, and these components. We also evaluated stand structure (e.g., stem density) in each stand type to discuss the changes in C stocks and NECB.

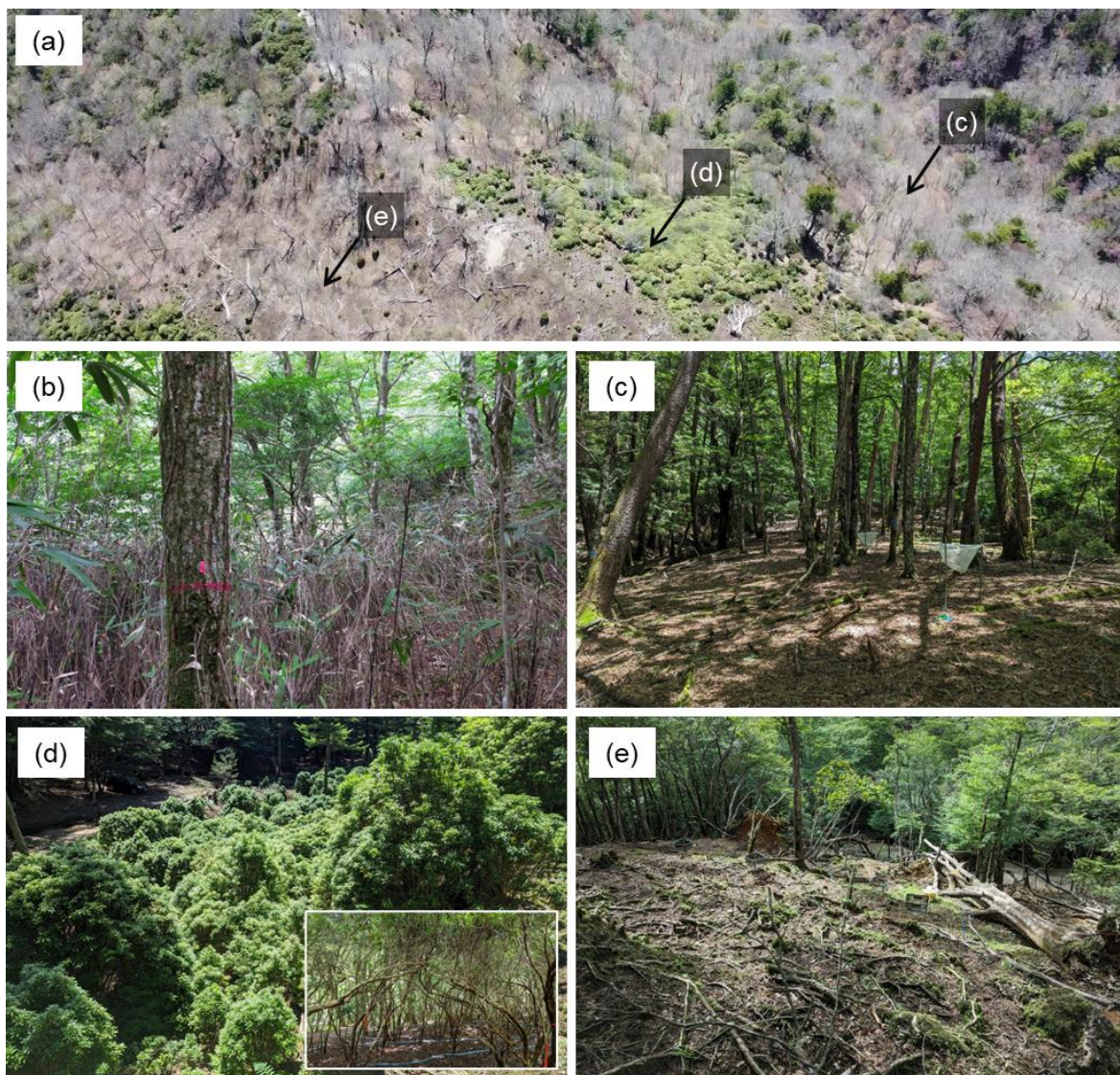


Fig. 5-1. Photographs of (a) multiple stand structural alterations within the landscape caused by deer in southern Kyushu Island, Japan, and example of study plots (b-e). Panel b shows broadleaf-conifer mixed stands with presence of understory vegetation (PU) which have not been affected by overbrowsing. Panel c shows mixed stands with no understory vegetation (NU) due to understory degradation. Panel d shows stands dominated by shrubs, Asebi (*Pieris japonica*) (SR) due to the expansion of unpalatable species. Panel e shows stands with canopy gap areas (CG) where the overstory trees have died and fallen, leaving no palatable juvenile trees. Note that there were no PU in panel (a) because PU remains limited areas such as the inside of the deer-exclosure fences.

5.2. Methods

5.2.1. Study area and experimental design

This study was conducted in SRF (Fig. 5-2). The details of SRF are described in chapters 1 and 4. We measured air temperature and precipitation during the year beginning March 20, 2023, using a temperature logger (S-THC-M002, Onset, MA, USA) and rain gauge (CTKF-1, Climatec, Tokyo, Japan) in the SRF (32°22'40.62" N; 131°6'9.20" E; 974 m above sea level). According to this, the mean annual temperature was 12.5°C, highest between July and August, and lowest between November and March (Fig. S5-1). Annual precipitation was 4381.3 mm, and daily precipitation often exceeded >60 mm (Fig. S5-1).

In this study, PU was assumed to represent stands that are unaffected by overbrowsing. NU was assumed to represent stands with their understory vegetation, including palatable juvenile trees, eliminated by deer (Enoki et al., 2013; Saruki et al., 2004). SR was assumed to represent stands formed by the expansion of unpalatable species (Tokumoto and Katayama, 2024). CG was assumed to represent stands that failed to regenerate palatable trees after overstory mortality (Shinoda and Akasaka, 2020). Based on these assumptions, we set the criteria for distinguishing between PU, NU, SR, and CG as follows. PU refers to a broadleaf–conifer mixed stand, where the understory vegetation covers an area of >100 m² (Fig. 5-1b). NU refers to a mixed stand without understory vegetation (Fig. 5-1c). SR refers to a stand dominated by Asebi (*P. japonica*), entirely covering the canopy in an area of >100 m² (Fig. 5-1d). Finally, CG refers to a stand with a canopy gap area in which the canopy is not closed in an area of >100 m² (Fig. 5-1e). We installed four 100–400 m² survey plots for each stand type that satisfied these criteria (Fig. 5-2). Each plot was determined for the following reasons. First, there were only four locations that fulfilled the criteria of PU. Of these, three were situated inside the deer exclusion fences installed by the SRF in 2003, 2013, and 2015, while the other was situated in one location where understory vegetation was maintained even outside the fence (Kawakami et al., 2020; Saruki et al., 2004). We thus installed PU plots in these locations. All PU plots were located on single slopes with angles of 8–37°. We then installed four each of NU, SR, and CG plots that could achieve the maximum plot size under the same topography as those for PU. Although the stand history of CG plots cannot be fully confirmed, the fact that many CWD have fallen or uprooted, and decay classes were well decomposed (class 3 or 4 from our results; see sections 5.2.2.2 and 5.3.2) suggests that CG plots were formed by canopy tree

decline that occurred in the last few decades and has been maintained until the present.

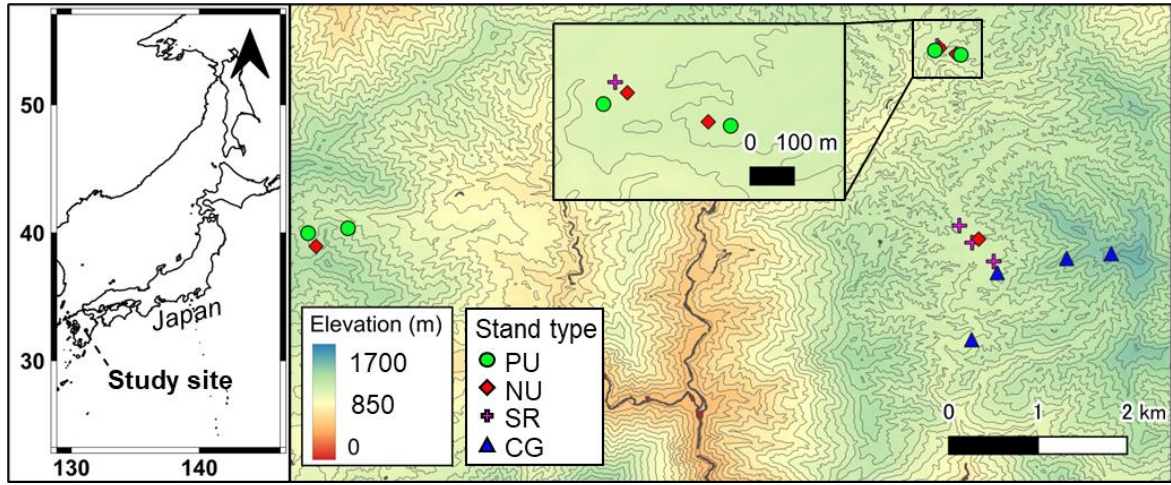


Fig. 5-2. Location of the study sites (left) and measurement plots (right). Contour intervals are 50 m and obtained from the Geospatial Information Authority of Japan.

5.2.2. Carbon stock estimates

In each plot, we estimated the C stock (g C m^{-2}) of overstory trees, understory vegetation, leaf litter, FWD, coarse woody debris (CWD), coarse roots, fine roots, and SOM by measuring the dry mass per unit area (g m^{-2}) and C concentration (g C g^{-1}) of each component. We considered overstory trees, understory vegetation, leaf litter, FWD, and CWD as aboveground C stocks (AGC). Coarse roots, fine roots, and SOM were considered belowground C stocks (BGC). The definitions of these components were described in chapter 1.

5.2.2.1. Measurements of overstory trees and understory vegetation

The inventory survey for overstory trees was conducted on July 6 to August 8, 2022, and July 10 to 22, 2023. All overstory trees were identified at the species level and measured for diameter (D) within the plots. The D of each tree, except Asebi, was measured at the breast height (DBH). For Asebi, D at 10 cm height (D_{10}) was measured because this species forms its crown at breast height, and DBH could not be measured. DBH and D_{10} were measured using steel tapes (PKM-20, TRUSCO, Tokyo, Japan) and vernier calipers (19989, Shinwa Rules Co., Ltd., Niigata, Japan).

Using the inventory survey data in 2022, the aboveground biomass of Asebi was estimated using an allometric equation established for the study area (Ichihashi and Katayama 2024):

$$\log_{10}(W_A) = 2.255 \log_{10}(D) + 1.533 \quad (\text{Eq. 5-1}),$$

where W_A is the individual-level aboveground biomass (g), and D is D_{10} (cm). Except for Asebi, the aboveground biomass was estimated using general allometric equations for Japanese tree species as follows (Ishihara et al. 2015):

$$\ln(W_A) = -1.196 + 1.622 \ln(D) + 0.338 \ln(D)^2 - 0.044 \ln(D)^3 + 0.708 \ln(\rho)$$

(Eq. 5-2),

where W_A is individual-level aboveground biomass (kg), D is DBH (cm), and ρ is species-specific wood gravity (g m^{-3}). Literature values collected from cool temperate forests in Japan were used for ρ values (Nakai and Yamai 1982; Andoh et al. 1990; Komiyama et al. 2011; Umebayashi et al. 2011) (Table S5-1). Genus- and family-level average values were used when literature values were unavailable. The biomass was converted to C mass using C concentration as a constant value in the literature (0.480 g C g^{-1}) (Martin et al. 2018). Based on the species list of palatability for the sika deer diet (Hashimoto and Fujiki 2014), the overstory tree species were divided according to their palatability for deer: Asebi (*P. japonica*), *Illicium anisatum*, and *Skimmia japonica* were classified as unpalatable species, and the other tree species were classified as palatable.

For sampling understory vegetation, we set up eight subplots with an area of $0.5 \text{ m} \times 0.5 \text{ m}$ per plot (i.e., 4 stand types $\times$ 4 plots $\times$ 8 subplots = 128 subplots, total sampling area per plot = $0.025 \times 8 = 0.2 \text{ m}^2$). The subplots were placed approximately 1 m outside the plot on the right and left sides of the slope. We sampled all understory vegetation in the subplots from August 1 to 6, 2022, and dried them in a dry oven (DKN812, Yamato Scientific, Japan) at a constant temperature of 70°C for two days. After drying, the samples were pooled for each plot. Samples were separated into tree seedlings, dwarf bamboo, mosses, ferns, and other herbs and weighed. A portion of the sample was then milled, and their C concentrations were measured using a C/N corder (Macro Corder JM1000CN, J-Science Lab, Kyoto, Japan) (Table S5-2).

5.2.2.2. Measurements of leaf litter, fine woody debris, and coarse woody debris

Leaf litter, FWD, and CWD were sampled from November 22 to December 5, 2022. Leaf litter and FWD were sampled in subplots with an area of $0.5 \text{ m} \times 0.5 \text{ m}$ at the corners and center of each plot (i.e., 4 stand types $\times$ 4 plots $\times$ 5 subplots = 80 subplots, total sampling area per plot = $0.025 \times 5 = 0.125 \text{ m}^2$). Sampled leaf litter and FWD were dried in the oven at 70°C for two days and weighed. C concentrations in leaf litter and FWD were measured using samples collected from each stand type (Table S5-3).

In the entire area of each plot, the decay class and species type (broad leaf or conifer) were

identified for all CWD. We used a six-level decay classification system, namely, 0, 1, 2, 3, 4, and 5, where 0 is the initial state of decomposition, and 5 is well-decomposed, following the National Forest Soil C Inventory methods in Japan (Ugawa et al., 2012). Wet weights were measured in the field for each species type and decay class for downed CWD with a diameter <10 cm (CWD_{log_small}). The wet weight of CWD_{log_small} was measured using a spring scale (74459; Shinwa Rules Co. Ltd., Niigata, Japan). When CWD_{log_small} crossed the edge of the plot, only a portion within the plot was cut and measured. Samples equivalent to approximately 10% of the total wet weight of each species type and decay class were transported to the laboratory as subsamples. The subsamples were dried in the oven at 70 °C for one week and weighed. The subsamples' dry/wet weight ratio was used to convert the sum of the wet weight of CWD_{log_small} to the dry mass. The dry mass of standing CWD (CWD_{snag}) and downed CWD with a diameter >10 cm (CWD_{log_big}) was estimated by multiplying the stem volume (m^3) by wood density ($g\ m^{-3}$). The stem volumes for CWD_{snag} and CWD_{log_big} were calculated as conic-paraboloids (Fraver et al. 2007):

$$V = \frac{L(5A_b + 5A_u + 2\sqrt{A_b A_u})}{12} \quad (\text{Eq. 5-3}),$$

where L , A_b , and A_u are the length (m) and cross-sectional area (m^2) of the base and upper ends of the CWD, respectively. We used literature values for decay class-specific wood densities calculated for Japanese trees (Ugawa et al., 2012). L , A_b , and A_u of CWD_{snag} and CWD_{log_big} were measured using steel tapes and a laser rangefinder (True Pulse 360, Laser Technology, Inc., Colorado, USA) within the plots. The A_u of a CWD_{snag} with a height >2 m was assumed to be 3 cm, which is the minimum definition size of the CWD. C concentration was used as a constant value in the literature ($0.485\ g\ C\ g^{-1}$) (Martin et al., 2021).

5.2.2.3. Measurements of coarse roots, fine roots, and soil organic matters

The dry mass of coarse roots was estimated using the general allometric equations for Japanese tree species (Ishihara et al., 2015):

$$\ln(W_c) = -3.274 + 2.315 \ln(D) \quad (\text{Eq. 5-4}),$$

$$\ln(W_c) = -3.432 + 2.224 \ln(D) \quad (\text{Eq. 5-5}),$$

$$\ln(W_c) = -3.786 + 2.345 \ln(D) \quad (\text{Eq. 5-6}),$$

where B_c is the individual-level coarse root biomass (kg), and D is the DBH and D_{10} (cm). Equations 5-4, 5-5, and 5-6 represent the equations for tree species of deciduous angiosperms,

evergreen angiosperms, and evergreen gymnosperms, respectively. For Asebi, we assumed that the estimated value of coarse root biomass using Eq. 5-5 would be overestimated. This is because the value of aboveground biomass estimated using the general allometric equations of Ishihara et al. (2015) was approximately 4-fold higher than that using the allometric equation of Ichihashi and Katayama (2024) (Fig. S5-2). Therefore, we corrected the estimated value of the coarse root biomass of Asebi using the following conversion equation:

$$W_{Cc} = 37.30 + 0.026W_{Ci} \quad (\text{Eq. 5-7}),$$

where W_{Cc} is the corrected coarse root biomass of Asebi, and W_{Ci} is the coarse root biomass of Asebi estimated using Eq. 5-5. We constructed Eq. 5-7 using regression analysis of individual-level aboveground biomass estimates by Ichihashi and Katayama (2024) and Ishihara et al. (2015) (Fig. S5-2).

For obtaining fine roots and mineral soil, soil cores (5 cm in diameter and 30 cm in depth) were collected from five points where leaf litter and FWD were collected in each plot. Soil cores were divided at three depth intervals of 0–10, 10–20, and 20–30 cm and oven-dried for 1 day at 105 °C. After drying, the samples were sieved through a 2-mm mesh and divided into fine roots and mineral soils. The C concentration of fine roots was measured using samples from each stand type and sampling depth (Table S5-3). The C stock of SOM was calculated using a depth-based approach as follows:

$$C_s = D_b L_s C_c \quad (\text{Eq. 5-8}),$$

$$D_b = \frac{M_s}{V}$$

$$(\text{Eq. 5-9}),$$

where C_s is the C stock of SOM (g C m^{-2}), D_b is the bulk density of the mineral soil (g m^{-3}), L_s is the sampling length of each soil layer (0.1 m in this study), C_c is the C concentration of the mineral soils (g C g^{-1}), M_s is the sampled mineral soil mass (g), and V is the sampling volume (m^3). In each plot, soil samples from each depth were pooled and measured for C_c (Fig. S5-3a).

5.2.3. Net ecosystem carbon balance estimates

This study calculated NECB by subtracting HR and SE from NPP:

$$B = P_n - R_h - S_e \quad (\text{Eq. 5-10}),$$

where B is NECB ($\text{g C m}^{-2} \text{ yr}^{-1}$), P_n is NPP ($\text{g C m}^{-2} \text{ yr}^{-1}$), R_h is HR ($\text{g C m}^{-2} \text{ yr}^{-1}$) and S_e is SE

(g C m⁻² yr⁻¹). The NECB in each plot was measured as follows.

5.2.3.1. Estimation of net primary production

The NPP was estimated using Eq. 1-2 such as sum of the stand increment of overstory woody biomass (I_o), the stand increment of aboveground understory biomass (I_u), the above-ground litter production (L), and the fine root production (F_r).

Using the inventory survey data in 2022 and 2023, the I_o was estimated by tracking individual tree growth as follows (Clark et al. 2001):

$$I_o = \frac{\sum G_s + \sum G_n}{A} \quad (\text{Eq. 5-11}),$$

where G_s is the annual woody biomass growth of surviving trees (g yr⁻¹), G_n is the woody biomass growth of trees that reached the minimum height (2 m) during the study period (g yr⁻¹), and A is an area of the study plot (m²). G_n was calculated as the total value of individual tree biomass that was newly recorded in 2023, using Eqs. 5-4 to 5-7 and Eqs. 5-12 to 5-16. Note that G_n includes biomass growth before the measurement period, although this study ignores it due to the low biomass values of trees less than 2 m in height. G_s were calculated as the difference of the biomass in stem (W_s), branch (W_b), and coarse root (W_c) between 2022 and 2023. The W_c was calculated using Eqs. 5-4 to 5-7. The W_s and W_b for Asebi were estimated using an allometric equation reported by Ichihashi and Katayama (2024):

$$\log_{10}(W_s + W_b) = -1.6586 + 2.3696 \log_{10}(D) \quad (\text{Eq. 5-12}),$$

where W_s is dry mass of stem (kg), W_b is dry mass of branch (kg), and D is D_5 (cm). Except for Asebi, the W_s and W_b were estimated in the equations proposed by Ishihara et al. (2015):

$$\ln(W_s) = -1.515 + 1.647 \ln(D) + 0.380 \ln(D)^2 - 0.056 \ln(D)^3 + 0.81 \ln(\rho) \quad (\text{Eq. 5-13}),$$

$$\ln(W_b) = -4.314 + 2.502 \ln(D) \quad (\text{Eq. 5-14}),$$

$$\ln(W_b) = -3.964 + 2.400 \ln(D) \quad (\text{Eq. 5-15}),$$

$$\ln(W_b) = -4.189 + 2.276 \ln(D) \quad (\text{Eq. 5-16}),$$

where D is DBH (cm), and ρ is species-specific wood gravity (g m⁻³). Eqs. 5-14, 5-15, and 5-16 represent the equations for tree species of deciduous angiosperms, evergreen angiosperms, and evergreen gymnosperms, respectively.

The I_u was estimated as the deviation of understory biomass between 2022 and 2023. Given that there was no understory vegetation in NU and only a few moss patches in CG (Fig.

S5-4), we assumed that I_u was zero in NU and CG. To obtain understory vegetation biomass data in 2023, we set eight subplots with an area of $0.5 \text{ m} \times 0.5 \text{ m}$ per plot in PU and SR. The subplots were placed approximately 2–3 m outside the plot on the right and left sides of the slope, and avoided subplots for sampling understory biomass in 2022. In SR, we harvested understory vegetation inside the subplot on July 17 to 20, 2023. In PU, instead of harvesting, we recorded the number of culms of dwarf bamboo (N, m^{-2}), the culm height of dwarf bamboo (H_d, m), the vegetation coverage of understory vegetation excluding dwarf bamboo (S, m^{-2}), and the community height of understory vegetation excluding dwarf bamboo (H_o, m) inside the subplot. This approach was taken to minimize the impact of destructive sampling on the vegetation in the plots and the surrounding area, because PU is distributed in only a few locations in the study area. The understory vegetation biomass in PU was estimated as follows:

$$W_d = 15.928NH_d + 335 \quad (\text{Eq. 5-17}),$$

$$W_o = 2706.3SH_o - 108.39 \quad (\text{Eq. 5-18}),$$

where W_d and W_o are the biomass (g m^{-2}) of dwarf bamboo and other understory vegetation, respectively. Eqs. 5-17 and 5-18 were created based on the biomass data obtained in 2022 (Fig. S5-5).

The L was estimated by fallen litter sampling. We placed four litter traps at the corners of each plot in September 2022, except for CG. Due to the difficulty of site access caused by landslides during the study period, there were two plots in CG where four litter traps were installed. Litter traps in PU, SR, and CG covered an area of 0.16 m^2 each and were placed 30 cm above the ground to collect understory vegetation litter. Litter traps in NU covered an area of 1 m^2 each and were placed 1 m above the ground. We collected the contents of the traps bi-monthly from March 2023 to March 2024. The contents included leaves, twigs, flowers, and seeds, excluding insect droppings. The contents were oven-dried and separated into understory herbs (i.e., dwarf bamboo and other herbs), Asebi, and other tree species. Contents that had fragmented to inseparability was classified as inseparable. For the L of the CG plots without litter traps, the average value of L obtained from the two plots with litter traps was used.

The R_f was estimated by the ingrowth core method (Vogt and Persson 1991; Katayama et al. 2019; Shimono et al. 2022). We installed ingrowth core bags (5 cm in diameter, 30 cm in depth, and 4 mm in mesh size) in vacated soil holes by sampling fine roots and SOM at each plot (i.e., 4 stand types $\times$ 4 plots $\times$ 5 points = 80 points). The core bags were installed on October 30, 2022, and in-situ incubated until November 4, 2023. After the incubation, we collected the

core bags and picked up living fine roots (diameter ≤ 2 mm) from the core bags. Fine roots were dried and separated into understory herbs, Asebi, and other tree species. No inseparable roots were present.

5.2.3.2. Estimation of heterotrophic respiration

The HR was estimated as the sum of HR from surface litter and SOM (R_{h_ss}) as well as CWD (R_{h_CWD}):

$$R_h = R_{h_ss} + R_{h_CWD} \quad (\text{Eq. 5-19}).$$

For estimating R_{h_ss} , a 600 m² experiment plot was established in SRF on March 2, 2024 (32°20'53"N, 131°5'32"E, 880 m above sea level) (Fig. 5-3a, b). One deer exclosure fence was located in this experimental plot (Fig. 5-3b). Areas inside the fence were covered by dwarf bamboo (Fig. 5-3c). There was no understory vegetation in the wider area outside the fence (Fig. 5-3d). Asebi was patchy distributed in outside areas with open-canopy sparse areas without overstory trees (Fig. 5-3e). Therefore, we installed CO₂ efflux measurement points inside the fence as PU and outside of the fence as NU and SR (Fig. 5-3b). Three CO₂ efflux measurement points were installed in each stand type (i.e., three stand types $\times$ three-point replications = 9 locations) on March 16, 2022 (Fig. 5-3b). We employed a micro-trenching method to measure R_{h_ss} (Riutta et al. 2021); for this method, polyvinyl chloride (PVC) collars (14.5 cm in diameter and 45 cm in height) were installed at each measurement point. Installed PVC collars were exposed 5 cm above the ground surface. The collars were allowed to stabilize for 18 weeks before the data collection started. The R_{h_ss} at each measurement point was measured by a closed static chamber (HL-1019A, Fuxin Gongda Hualian Technology Co., Ltd., Liaoning, China) (Kuriyama et al. 2021; Wang et al. 2022). The chamber system consisted of a cylindrical chamber (soil exposure area: 165 cm², chamber volume: 3300 cm³), an infrared gas analyzer, and a fan that circulates the air in the chamber in one unit. The system automatically recorded CO₂ efflux (F , $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 20-minute intervals. In each recording period, soil temperature (°C) and soil volumetric water content (SVWC, %) at 5 cm depth near the chamber were automatically measured from a thermometer and a time domain reflectometer sensor. Measurements were conducted during six campaigns from 2022 to 2023 (August 5 to October 6, 2022; November 14 to December 4, 2022; February 14 to February 28, 2023; March 14 to April 10, 2023; July 10 to August 31, 2023; and October 30 to November 8, 2023). In each campaign, the chamber was relocated to different points every 1–2 days until measurements were completed at all points. During the campaign, CO₂ efflux measurement was suspended

when it became difficult to conduct, such as under heavy rainfall and when road access was blocked.

We examined the relationships of R_{h_ss} with soil temperature and SVWC for each stand type. This was done using three empirical equations. The first equation expresses the exponential relationship using soil temperature (Lloyd and Taylor 1994):

$$F = a \exp(bT) \quad (\text{Eq. 5-20}),$$

where T is soil temperature ($^{\circ}\text{C}$) at 5 cm depth, and a and b are constants. The second equation expresses quadric relationships using SVWC (Saiz et al. 2006):

$$F = c + d\theta + f\theta^2 \quad (\text{Eq. 5-21}),$$

where θ is SVWC (%) at 5 cm depth, and c , d , and f are constants. The third equation expresses the exponential power relationships using T and θ (Saiz et al., 2006):

$$F = g \exp(hT) \theta^i \quad (\text{Eq. 5-22}),$$

where g , h , and i are constants. To estimate the constants in Eqs. 5-20 to 5-22, non-linear mixed-effect models (Lindstrom and Bates 1990) were applied to pooled data from the three measurement points for each understory type. Thus, all constants in Eqs. 5-20 to 5-22 consisted of fixed and random effects. Fixed effects were expressed as representative constants in each understory type. Random effects were assigned to differences in measurement points in each understory type. Constants were fitted using a maximum likelihood procedure. The goodness of fit was evaluated with the Akaike information criterion (AIC), and the coefficient of determination was explained by fixed effects (Marginal R^2) (Spiess and Neumeyer 2010). The analyses were conducted using R software version 4.2.2 for Windows 10 x64 (R Core Team 2024) with the packages “nlme” (Pinheiro et al. 2017) and “nlraa” (Miguez 2021).

Continuous soil temperature records were substituted into the fitted temperature-driven soil respiration model (i.e., Eq. 5-20). The models including SVWC (i.e., Eqs. 5-21 and 5-22) were not used for this estimation because of the lower contribution of SVWC to the temporal dynamics of R_{h_ss} in this study (see Table 5-4). For obtaining continuous soil temperature records, one plot in each of PU, NU, SR, and CG was selected to record soil temperature among study plots (Fig. 5-2). The soil temperature was recorded at 30-minute intervals from 2022 to 2023 with a thermometer at 10 cm depth (S-TMB-M002, Onset, MA, USA). We calculated the representative annual R_{h_ss} based solely on the fixed effect of the model. Note that this study did not measure R_{h_ss} in CG; therefore, the temperature– R_{h_ss} relationships in NU was adopted as the relationship in CG instead.

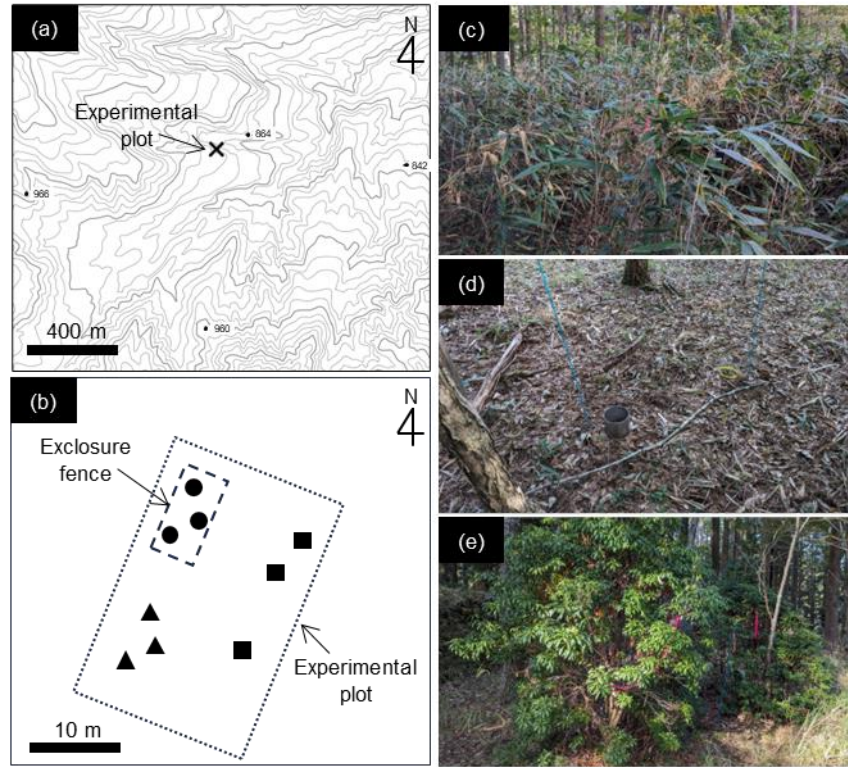


Fig. 5-3. Location of the experimental plot (a), map of the plot (b), and photographs of stand types (c–e). In panel b, dots represent the CO₂ efflux measurement points. Circles represent the points for PU (c), triangles represent the points for NU (d), and squares represent the points for SR (e).

The R_{h_CWD} was estimated using the equation proposed by Dai et al. (2021):

$$R_{h_CWD} = M - M \exp(-kt)$$

$$k = 0.273 + 0.00000668T_a + 0.00000223P - 0.00370L_a - 0.0000383E + 0.0000678S \quad (\text{Eq. 5-23}),$$

where M is C stock of CWD (g C m^{-2}), k is decay constant ($\text{g g}^{-1} \text{yr}^{-1}$), T_a is mean annual air temperature ($^{\circ}\text{C}$), P is annual precipitation (mm), L_a is latitude ($^{\circ}\text{N}$), and S is annual snowfall (kg m^{-2}). We calculated R_{h_CWD} in each plot. Parameters T_a and P in each plot were obtained from 1 km^2 mesh climate data (<https://www.jma.go.jp/jma/en/menu.html>). S was assumed to be zero for all plots. Although decay constant k included the effect of fragmentation and leaching in addition to the biological decomposition, we ignored the effect of fragmentation and leaching because this contribution to k was 0.61 % (Dai et al. 2021).

5.2.3.3. Estimation of soil carbon loss by erosion

The SE was estimated by multiplying annual eroded soil depth ($\text{cm}^{-1} \text{yr}^{-1}$) and C stock of

SOM:

$$S_e = ES_c \quad (\text{Eq. 5-24}),$$

where E is annual eroded soil depth ($\text{cm}^{-1} \text{yr}^{-1}$), and C_s is C stock of SOM ($\text{g C m}^{-2} \text{cm}^{-1}$). The C_s in each plot was obtained in section 5.2.2.3. The E was measured by tracking the eroded depth of iron pins (Hart et al. 2017; Gholami et al. 2021). From October 4 to 6, 2022, we inserted 16 pins in each plot (i.e., 4 stand types $\times$ 4 plots $\times$ 16 pins = 256 pins). Pins were 2.8 cm in diameter and 25 cm in length. Each pin was placed at least 1 m away from each other. Pins were inserted approximately 15 cm into the soil. The boundary between the pin and the mineral soil (excluding surface litter) was marked. Pins were in-situ incubated until October 30 to November 4, 2023. After the incubation, the E was measured as the vertical distance from the mineral soil layer to the marked lines of the pin. The E of pins that were buried by sediment from upslope was recorded to 0 cm. Such buried pins do not exist in PU, and there was one pin in NU, two pins in SR, and two pins in CG. In addition, some of the pins were clearly pulled out or embedded in the ground by animals, including deer. These pins were excluded from the measurement. The number of pins used in the analysis was 129 pins. The slope angle ($^\circ$) on the place of each pin was also recorded to consider the effect of the slope angle on E .

5.2.4. Comparison of stand structure, carbon stocks, and net ecosystem carbon balance

Using PU as a baseline, we evaluated whether the changes in stand structural variables, C stocks, and NECB components were significant for each stand type. This evaluation was performed using a Dunnett test. This statical test was conducted using R software version 4.2.2 for Windows 10 x64 (R Core Team, 2024) with the “*multcomp*” package version 1.4–20 (Bretz et al. 2010). Although the threshold for statistical significance was set at $p < 0.05$, due to the small sample size, $p < 0.10$ was also considered as a marginally significant difference.

5.3. Results

5.3.1. Stand structure

The stand structure differed for each stand type. The mean value and standard deviation (SD) of the mean stem diameter (i.e., D including DBH and D_{10}) were 13.3 ± 9.8 cm in PU, 17.4 ± 9.0 cm in NU, 4.4 ± 1.2 cm in SR, and 17.8 ± 19.0 cm in CG (Table 5-1). The canopy height was 15.6 ± 1.9 m in PU, 16.8 ± 2.6 m in NU, and 4.1 ± 1.1 m in SR (Table 5-1). The stem density in SR was 4.6-fold higher than that in PU, and this difference was significant ($p = 0.001$). The stem density in SR was characterized by a high density of unpalatable trees (i.e., Asebi) with $D < 10$ cm (7430.6 ± 2695.7 stems ha^{-1} , accounting for 47.6% of total stem density) (Fig. 5-4). There were fewer palatable trees in NU, SR, and CG, especially those with $D < 10$ cm, than in PU (Fig. 5-4). Palatable trees with $D < 10$ cm accounted for 38.1% of the total stem density in PU, while they comprised less than 10% in other stand types (NU: 9.6% of the total, SR: 0.4% of the total, CG: 0% of the total).

Table 5-1. Mean (SD) values of stand structure for each stand type. Letters * and † indicate significant ($p < 0.05$) and marginally significant ($p < 0.10$) differences compared to the PU, respectively, based on the two-sided Dunnett test.

Stand types	PU	NU	SR	CG
Slope angle (°)	21.6 (12.1)	18.4 (8.8)	16.3 (11.9)	19.9 (7.0)
Stand age ^a	101.0 (6.2)	112.8 (20.0)	50.0 (14.4) *	N/A
Species richness ^b	13.8 (3.5)	12.0 (7.1)	2.5 (2.4) *	1.2 (0.5) *
Canopy height (m) ^c	15.6 (1.9)	16.8 (2.6)	4.1 (1.1) *	N/A
Stem density (ha^{-1})	3410.4 (3622.6)	1531.2 (1128.9)	15619.4 (5325.9) *	107.1 (29.4)
Mean diameter (cm) ^d	13.3 (9.8)	17.4 (9.0)	4.4 (1.2)	17.8 (19.0)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	41.5 (3.0)	36.9 (6.7)	44 (30.7)	5.9 (6.8) *

Superscript a: stand age was determined by sampling tree-ring cores of the three largest trees in each plot and counting the number of annual rings. The stand age in CG was not measured to avoid damage to the residual trees from the tree-ring core sampling.

Superscript b: number of species for overstory trees

Superscript c: canopy height measured using a laser rangefinder. The canopy height in CG was not measured because the canopy was not closed.

Superscript d: mean diameter calculated from the diameter at 10 cm height (D_{10}) of Asebi (*Pieris japonica*) and the diameter at breast height (DBH) of other species.

5.3.2. Carbon stocks

Lower total C stocks were observed in SR and CG than in PU but not in NU, mainly because of the decrease in AGC (Table 5-2, Fig. 5-5). The total C stocks in NU ($20683.6 \pm 4152.2 \text{ g C m}^{-2}$) were comparable to that in PU (25190.5 ± 3065.1 , $p = 0.600$). Meanwhile, the total C stocks in SR (14162.5 ± 6561.1) and CG (12953.1 ± 6160.3) were 44% and 49% lower than those in PU, respectively. These differences were marginally significant for SR ($p = 0.063$) and significant for CG ($p = 0.033$). The AGC was highest for PU ($13300.9 \pm 1598.7 \text{ g C m}^{-2}$), followed by NU (10952.1 ± 1765.3), SR (6413.9 ± 5196.7), and CG (5398.6 ± 4352.0). The AGC in SR and CG was 52% and 59% lower than that in PU, respectively, and these differences were significant (NU; $p = 0.687$, SR; $p = 0.047$, CG; $p = 0.023$). The overstory tree was the most dominant component of AGC in PU, NU, and SR, whereas CWD was the most dominant component of AGC in CG. Meanwhile, there were no significant differences in BGC between PU ($11889.6 \pm 2054.0 \text{ g C m}^{-2}$) and other stand types (NU; 9731.6 ± 2773.4 , $p = 0.584$, SR; 7911.3 ± 3988.1 , $p = 0.162$, CG; 7369.4 ± 1981.3 , $p = 0.103$). SOM was the most dominant component of the BGC for all stand types.

The C stock of overstory trees in NU ($10198.5 \pm 1651.0 \text{ g C m}^{-2}$) was comparable to that in PU (11890.7 ± 1136.6 , $p = 0.810$, Table 5-2, Fig. 5-5). Meanwhile, the results in SR ($5350.8 \pm 5819.8 \text{ g C m}^{-2}$) and CG (2029.1 ± 2343.1) were 55% and 83% lower than that in PU, respectively. These differences were significant (SR; $p = 0.04$, CG; $p < 0.01$). The reduction in overstory trees was driven by the difference in the C stocks of palatable trees with $D > 10 \text{ cm}$ (Fig. 5-4). The C stock of palatable trees with $D > 10 \text{ cm}$ in SR ($4228.4 \pm 5289.0 \text{ g C m}^{-2}$) and CG (2028.9 ± 2343.4) was 63% and 82% lower than that in PU (11510.3 ± 1175.2), respectively. The contribution of trees with $D < 10 \text{ cm}$ to the total overstory C stock was negligible in all stand types. Although Asebi with $D < 10 \text{ cm}$ was dominant in SR, the contribution of Asebi with $D < 10 \text{ cm}$ was 5.9% of the total overstory C stock ($317.5 \pm 75.1 \text{ g C m}^{-2}$).

The C stock of understory vegetation in NU ($3.5 \pm 7.0 \text{ g C m}^{-2}$) was 99% lower than that in PU (634.5 ± 671.3), and this difference was marginally significant ($p = 0.072$, Table 5-2, Fig. S5-4). Meanwhile, the results in SR ($195.5 \pm 241.3 \text{ g C m}^{-2}$) and CG (81.1 ± 105.1) were comparable to those in PU (SR; $p = 0.250$, CG; $p = 0.121$). By growth form, dwarf bamboo dominated understory vegetation in PU, whereas seedlings of Asebi and moss species dominated SR and CG, respectively (Fig. S5-4).

The C stock of leaf litter in NU, SR, and CG was lower than that in PU but not in the C

stock of FWD (Table 5-2). The C stock of leaf litter in NU ($270.7 \pm 64.8 \text{ g C m}^{-2}$), SR (255.8 ± 74.2), and CG (108.5 ± 38.7) were 36–74% lower than that in PU (422.5 ± 104.1). These differences were significant (NU; $p = 0.034$, SR; $p = 0.021$, CG; $p < 0.001$). The C stock of CWD in NU ($377.8 \pm 40.0 \text{ g C m}^{-2}$) and SR (527.3 ± 846.4) were comparable to that in PU (238.5 ± 109.7) (NU; $p = 0.999$, SR; $p = 0.989$, Table 5-2, Fig. S5-6). Meanwhile, the result in CG ($3102.2 \pm 3210.6 \text{ g C m}^{-2}$) was 13-fold higher than that in PU. This difference was marginally significant ($p = 0.077$). CWD in CG was mainly CWD_{log_big} with decay classes 3 and 4 (Fig. S5-6).

Table 5-2. Mean (SD) values of carbon stocks for each stand type. Letters * and † indicate significant ($p < 0.05$) and marginally significant ($p < 0.10$) differences compared to the PU, respectively.

	PU	NU	SR	CG
Total C stocks	25190.5 (3065.1)	20683.6 (4152.2)	14162.5 (6561.1) †	12953.1 (6160.3) *
Aboveground C stocks	13300.9 (1598.7)	10952.1 (1765.3)	6413.9 (5196.7) *	5398.6 (4352.0) *
Overstory tree	11890.7 (1136.6)	10198.5 (1651.0)	5350.8 (5819.8) *	2029.1 (2343.1) *
Understory vegetation	634.5 (671.3)	3.5 (7.0) *	195.5 (241.3)	81.1 (105.1)
Leaf litter	422.5 (104.1)	270.7 (64.8) *	255.8 (74.2) *	108.5 (38.7) *
Fine woody debris	112.9 (59.4)	101.6 (44.0)	84.5 (43.5)	77.6 (66)
Coarse woody debris	238.5 (109.7)	377.8 (40.0)	527.3 (846.4)	3102.2 (3210.6) †
Belowground C stocks	11889.6 (2054)	9731.6 (2773.4)	7911.3 (3988.1)	7369.4 (1981.3)
Overstory coarse roots	2643.5 (439.9)	2567.6 (647.4)	1159.6 (1182.6) *	449.2 (518.4) *
Fine roots	122.9 (57.5)	133.9 (74.8)	84.2 (28.2)	28.6 (23.1) †
Soil organic matters	9123.2 (2025.8)	7030.1 (2911.0)	6667.5 (2964.2)	6891.6 (1498.8)
0–10 cm	3600.7 (868.2)	2169.9 (595.1) *	2209.9 (656.7) *	2559.0 (441.6)
10–20 cm	2742.9 (467.5)	2489.7 (1286.1)	2420 (963.1)	2031.2 (1331.5)
20–30 cm	2779.6 (1004.2)	2370.5 (1487.8)	2037.6 (1382.1)	2301.4 (308.4)

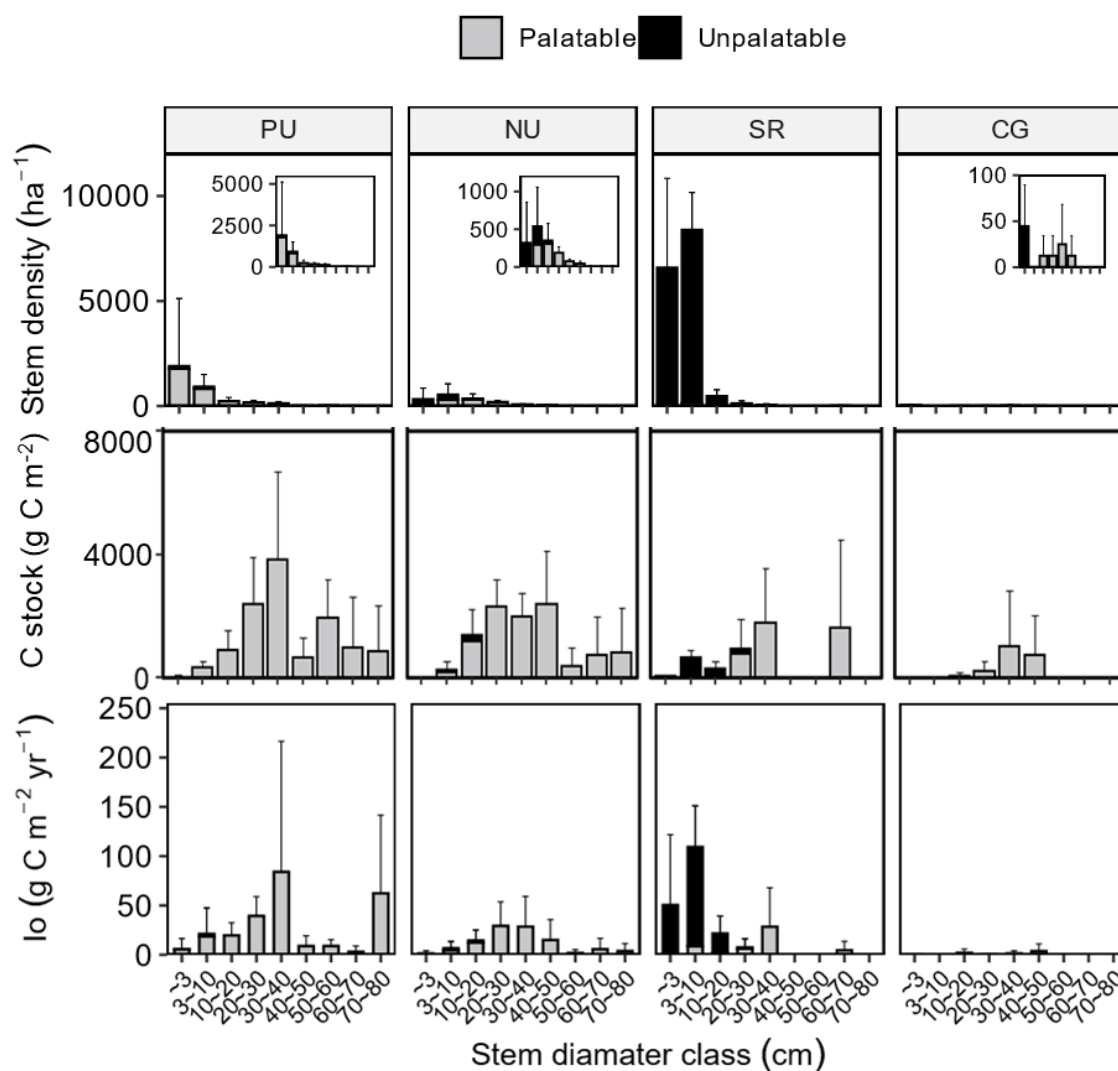


Fig. 5-4. Stem diameter (D) class distribution of stem density (a) and aboveground carbon stocks of overstory trees (b). Bars indicate the mean value for palatable or unpalatable tree species obtained from each plot. Error bars indicate the SD of the total value for each D class. Note that D includes the diameter at 10 cm height (D_{10}) of Asebi (*Pieris japonica*) and the diameter at breast height (DBH) of other tree species. Carbon stocks of overstory trees include leaves, twigs, and stems.

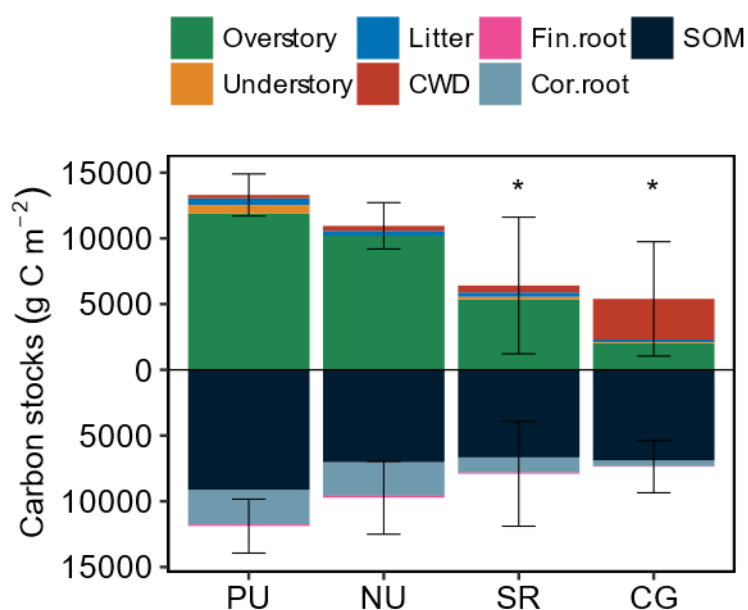


Fig.5-5. Stacked bar chart of above-ground (AGC) and below-ground carbon stocks (BGC). The bars indicate the mean value of each component. The error bars indicate the standard deviation of AGC and BGC. * Indicates $p < 0.05$ difference of AGC from PU based on the Dunnet test.

Abbreviation for carbon components: Overstory; above-ground overstory tree, Understory; above-ground understory vegetation, Litter; above-ground litters including leaf litter and fine woody debris, CWD; above-ground coarse woody debris (> 3cm central diameter), Fin.root; fine roots (< 2mm diameter) including overstory trees and understory vegetation; Cor.root; coarse roots including overstory trees, and SOM; soil organic matter in the mineral soil layer.

Compared to the results in PU, there was a lower C stock of coarse roots in SR and CG, as well as a lower C stock of fine roots in CG (Table 5-2, Fig. 5-5, Fig. S5-7). The C stock of coarse roots in SR ($1159.6 \pm 1182.6 \text{ g C m}^{-2}$) and CG (449.2 ± 518.4) were 56% and 83% lower than that in PU (2643.5 ± 439.9), respectively. These differences were significant (SR; $p = 0.042$, CG; $p = 0.004$). The C stock of fine roots in CG ($28.6 \pm 23.1 \text{ g C m}^{-2}$) was 77% lower than that in PU (122.9 ± 57.5) (Fig. S5-7). This difference was marginally significant ($p = 0.054$).

The C stock of SOM at the 0–30 cm depth in NU ($7030.1 \pm 2911.0 \text{ g C m}^{-2}$), SR (6667.5 ± 2964.2), and CG (6891.6 ± 1498.8) were not significantly different from PU (9123.2 ± 2025.8) (NU; $p = 0.500$, SR; $p = 0.381$, CG; $p = 0.452$, Table 5-2). Meanwhile, the C stock of SOM at the 0–10 cm depth in NU and SR was significantly lower than that in PU (NU, $p = 0.025$; SR, $p = 0.029$). The reduction of C stock of SOM at 0–10 cm depth was driven by the difference in soil C concentration (Fig. S5-3a). There was no significant difference in soil bulk

density between NU, SR, and CG compared to PU at any depth ($p > 0.05$) (Fig. S5-3b). Compared to the soil C concentrations at 0–10 cm depth in PU, the results in NU and SR were marginally significantly lower (NU, $p = 0.056$; SR, $p = 0.080$), and the results in CG was significantly lower ($p = 0.011$).

5.3.3. Net ecosystem carbon balance

5.3.3.1. Net primary production

Lower NPP was observed in NU and CG than in PU but not in SR, mainly due to decreased overstory biomass increment (i.e., I_o) (Table 5-3, Fig. S5-8). The NPP in NU (400.2 ± 85.7 g C m⁻² yr⁻¹) and CG (71.9 ± 15.3) were 45% and 90% lower than those in PU (721.9 ± 277.4), respectively. These differences were significant (NU; $p = 0.015$, CG; $p < 0.01$). Meanwhile, the NPP in SR (554.5 ± 91.8 g C m⁻²) was comparable to that in PU ($p = 0.162$).

The I_o was highest for PU (347.3 ± 180.9 g C m⁻² yr⁻¹), followed by SR (280.6 ± 97.0), NU (141.2 ± 63.4), and CG (9.8 ± 15.2) (Table 5-3, Fig. 5-4). The I_o in NU and CG was 59% and 97% lower than that in PU, respectively, and these differences were significant (NU; $p = 0.048$, CG; $p = 0.002$). The lower I_o in NU and CG was driven by the lower stem density of palatable trees (Fig. 5-4). In SR, the high stem density of Asebi with $D < 10$ cm led to high I_o , which was comparable to that of PU ($p = 0.718$) (Fig. 5-4).

There were no significant differences in above-ground litter production among PU (258.8 ± 74.8 g C m⁻² yr⁻¹), NU (193.2 ± 13.6 g C m⁻² yr⁻¹, $p = 0.227$), SR (177.7 ± 61.8 g C m⁻² yr⁻¹, $p = 0.127$), and CG (44.7 g C m⁻² yr⁻¹; SD and p -value was not calculated because this value was based on the results of 2 plots) (Table 5-3, Fig. S5-9). Further, no differences in fine root production were observed among PU (45.3 ± 20.2 g C m⁻² yr⁻¹), NU (65.8 ± 24.8 , $p = 0.361$), SR (34.7 ± 20.6 , $p = 0.792$), and CG (17.5 ± 10.5 , $p = 0.163$) (Table 5-3, Fig. S5-10).

Table 5-3. Mean (SD) values of net ecosystem carbon balance (NECB, g C m⁻² yr⁻¹) and its components for each stand type. Letters * and † in the carbon flux results indicate the result with $p < 0.05$ and $p < 0.10$ compared to the PU, respectively.

	PU	NU	SR	CG
NECB	307.0 (244.6)	-98.2 (92.3) †	97.3 (158.1)	-894.4 (442)*
NPP	721.9 (277.4)	400.2 (85.7) *	554.5 (91.8)	71.9 (15.3)*
I_o	347.3 (180.9)	141.2 (63.4) *	280.6 (97.0)	9.8 (15.2)*
I_u	70.5 (54.1)	0 ^a	61.4 (73.1)	0 ^a
L	258.8 (74.8)	193.2 (13.6)	177.7 (61.8)	44.7 ^b
F_r	45.3 (20.2)	65.8 (24.8)	34.7 (20.6)	17.5 (10.5)
HR	175.4 (12.1)	170.6 (5.0)	169.2 (95.6)	464.8 (324.8)*
R_{h_SS}	148.6	128.1	109.6	136.7
R_{h_CWD}	26.8 (12.1)	42.5 (5.0)	59.6 (95.6)	328.1 (324.8)*
SE	239.5 (97.7)	327.7 (73)	287.9 (101.8)	501.5 (219.4)*

Abbreviations: NECB; net ecosystem carbon balance, NPP; net primary production, I_o ; stand biomass increment of overstory trees, I_u ; stand biomass increment of understory vegetation, L ; above-ground litter production, F_r ; fine root production, HR; heterotrophic respiration, R_{h_SS} ; HR of surface litter and soil organic matter, R_{h_CWD} ; HR of coarse woody debris, and SE; soil carbon loss by sediment export.

Superscript a: the I_u in NU and CG was assumed to be zero because these stand types have no understory vegetation or have only small patches of moss species, respectively.

Superscript b: the L of the CG was measured on two plots. For the remaining two plots, where L was not measured, the average value of L was assumed. For this reason, the SD was not calculated, and statistical differences were not evaluated for L in CG.

5.3.3.2. Heterotrophic respiration

A consistent positive exponential response of HR from surface litter and SOM (i.e., R_{h_SS}) to soil temperature was observed for all stand types (Table 5-4). The R^2 values for the temperature model (i.e., Eq. 5-20) ranged from 0.84 to 0.92, suggesting that most of the variation in R_{h_SS} was explained by soil temperature. In contrast, the R^2 values for the SVWC model (i.e., Eq. 5-21) were less than 0.5 (0.015 to 0.48) (Table 5-4). Furthermore, the AIC and R^2 values for the hybrid model of temperature and SVWC (i.e., Eq. 5-22) did not differ from those of the temperature model (e.g., the results in PU had AIC = -5439.92 and R^2 = 0.84 for the temperature model, and AIC = -5611.54 and R^2 = 0.88 for the hybrid model) (Table 5-4).

Based on the temperature-driven model (i.e., Eq. 5-20, Table 5-4), annual R_{h_SS} and their seasonable trends were predicted (Fig. S5-11). The soil temperature in PU, NU, SR, and CG

showed consistent seasonal variation: it increased from March, peaked in July, and then decreased to the minimum value from January to March (Fig. S5-11). The seasonal variation of R_{h_ss} was similar to that of soil temperature. Annual R_{h_ss} was estimated to be $148.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ for PU, $128.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ for NU, $109.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ for SR, and $136.7 \text{ g C m}^{-2} \text{ yr}^{-1}$ for CG (Table 5-3, Fig. S5-12).

The total amount of HR in NU ($170.6 \pm 5.0 \text{ g C m}^{-2} \text{ yr}^{-1}$) and SR (169.2 ± 95.6) were comparable to that in PU (175.4 ± 12.1) (NU; $p = 0.764$, SR; $p = 0.768$) (Table 5-3, Fig. S5-12). In contrast, the result in CG ($464.8 \pm 324.8 \text{ g C m}^{-2} \text{ yr}^{-1}$) was significantly 2.6-fold higher than that in PU ($p = 0.04$). This difference was driven by the high amount of HR from CWD (i.e., R_{h_CWD}). The R_{h_CWD} in CG was $328.1 \pm 324.8 \text{ g C m}^{-2} \text{ yr}^{-1}$, about 12-fold higher than that in PU ($26.8 \pm 12.1 \text{ g C m}^{-2} \text{ yr}^{-1}$, $p = 0.033$) (Fig. S5-12).

5.3.3.3. Soil carbon loss by erosion

The SE in NU ($327.7 \pm 73.0 \text{ g C m}^{-2} \text{ yr}^{-1}$) and SR (287.9 ± 101.8) were comparable to that in PU (239.5 ± 97.7) (NU; $p = 0.366$, SR; $p = 0.544$) (Table 5-3, Fig. S5-13). The result in CG ($501.5 \pm 219.4 \text{ g C m}^{-2} \text{ yr}^{-1}$) was significantly about 2-fold higher than that in PU ($p = 0.023$). At individual erosion pin level, annual eroded soil depth (i.e., E) was positively related to slope angle regardless of the stand types (Fig. 5-6). The E at slope degree of 0 (i.e., the intercept of the regression line) and the sensitivity of E to slope angle (i.e., slope value of the regression line) were higher in NU, SR, and CG than in PU (Fig. 5-6). In addition, there was a negative relationship between plot-level E (the average E of each plot) and SOM at 0–10 cm, regardless of the stand type (Fig. 5-7). As a result, despite the high E values in NU and SR, the SE in NU and SR did not differ from PU due to the lower SOM.

5.3.3.4. Total balance

NECB was highest in PU ($307.0 \pm 244.6 \text{ g C m}^{-2} \text{ yr}^{-1}$), followed by SR (97.3 ± 158.1), NU (-98.2 ± 92.3), and CG (-894.4 ± 442) (Table 5-3, Fig. 5-8). These differences were marginally significant for NU ($p = 0.065$) and significant for CG ($p < 0.01$). Lower NECB for NU was mainly driven by lower NPP (Fig. 5-8). SR showed comparable NECB to PU due to the similar NPP (Fig. 5-8). CG showed the lowest NECB due to the lower NPP as well as higher HR and SE (Fig. 5-8).

Table 5-4. Estimated constants and their standard error (SE) as well as SD of random effects (RE). The value of n indicates the number of data points. The model terms T , θ , and $T \& \theta$ indicate soil temperature, soil volumetric water content, and hybrid temperature and water models, respectively (see Eqs. 5-20, 5-21, and 5-22). Values of R^2 are the marginal R^2 of the model.

PU (n = 1720)				NU (n = 1873)				SR (n = 2170)			
Fixed effect		SD of RE		Fixed effect		SD of RE		Fixed effect		SD of RE	
Constant	SE			Constant	SE			Constant	SE		
T (AIC = -4964.31, R^2 = 0.92)				T (AIC = -4176.56, R^2 = 0.91)				T (AIC = -5548.52, R^2 = 0.89)			
a	0.096	0.0030	0.0048	a	0.072	0.016	0.028	a	0.051	0.0059	0.010
b	0.10	0.0013	0.0020	b	0.11	0.010	0.017	b	0.12	0.0058	0.010
θ (AIC = -1829.85, R^2 = 0.49)				θ (AIC = 467.82, R^2 = 0.043)				θ (AIC = -830.63, R^2 = 0.015)			
c	4.6	1.6	2.7	c	-0.40	0.42	0.34	c	-0.44	0.22	0.30
d	-0.41	0.20	0.35	d	0.13	0.040	7.7×10^{-9}	d	0.093	0.021	0.021
f	0.010	0.0062	0.011	f	-0.0044	0.0012	0.00094	f	-0.0027	0.00055	8.2×10^{-9}
$T \& \theta$ (AIC = -4080.78, R^2 = 0.93)				$T \& \theta$ (AIC = -4277.68, R^2 = 0.92)				$T \& \theta$ (AIC = -5523.07, R^2 = 0.90)			
g	0.19	0.016	4.2×10^{-10}	g	0.33	0.046	0.079	g	0.069	0.0060	5.7×10^{-12}
h	0.097	0.0010	1.5×10^{-7}	h	0.11	0.0094	0.016	h	0.12	0.0044	0.0075
i	-0.21	0.026	6.3×10^{-7}	i	-0.53	0.026	0.040	f	-0.11	0.044	0.055

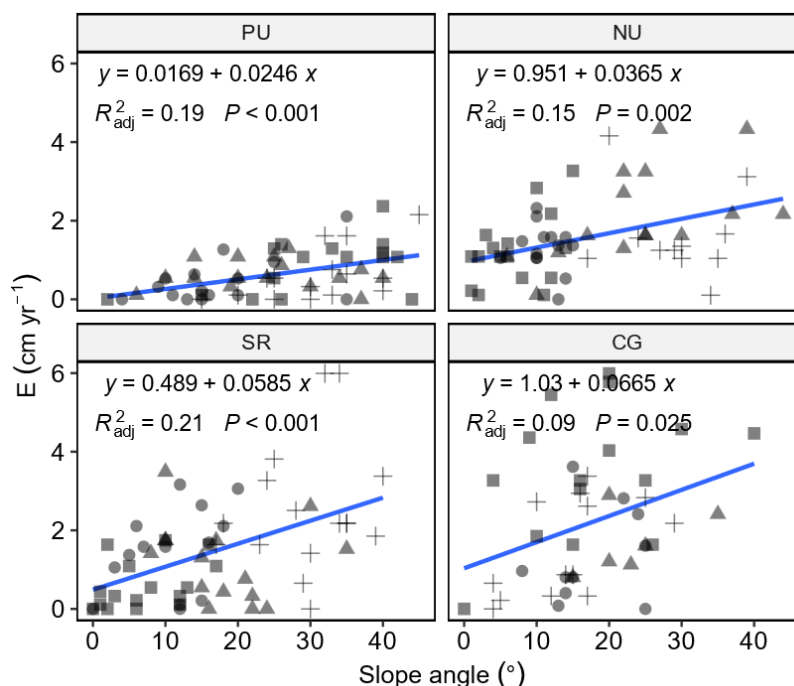


Fig. 5-6. Relationships between eroded soil depth (E) and slope angle in each stand type. Dots refer to the result of each pin. Symbols (circle, triangle, square, and cross) refer to the plot replicates in each stand type. The blue line indicates the regression line between E and the slope angle. The regression equation with adjusted R^2 and p -value were shown inside the graph.

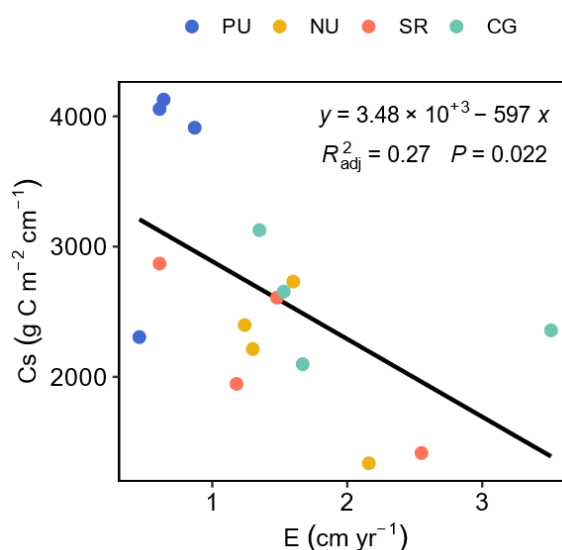


Fig. 5-7. Relationships between carbon stock of soil organic matter (C_s) and eroded soil depth (E) in each stand type. Dots refer to the result of each plot. The black line indicates the regression line. The regression equation with adjusted R^2 and p -value were shown inside the graph.

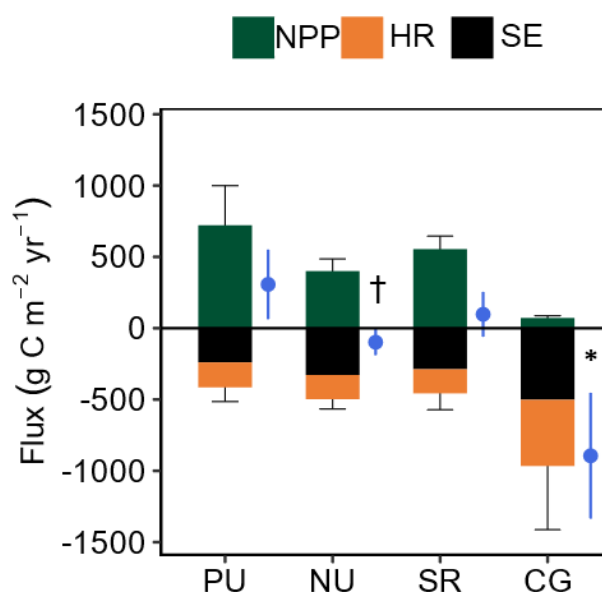


Fig. 5-8. Net ecosystem carbon balance (NECB) of each stand type. The stacking bars indicate the mean value of net primary production (NPP), heterotrophic respiration (HR), and soil carbon loss by sediment export (SE). Upper and lower error bars in stacking bars indicate the SD of NPP and the sum of HR and SE, respectively. Circles to the right of the stacking bars indicate NECB and its SD. Letters * and † indicate lower NECB from PU with $p < 0.05$ and $p < 0.10$, respectively, based on one-sided Dunnett's test.

5.4. Discussions

5.4.1. Impacts of overbrowsing-induced stand structural alteration on forest carbon sequestration

Deer overbrowsing promotes alteration from PU to NU by feeding on understory vegetation (Murata et al., 2009; Saruki et al., 2004). In NU with few overstory trees, further alterations from NU to SR and CG have been observed through the promotion of unpalatable species (Forbes et al., 2019; Tremblay et al., 2006) and inhibition of palatable sapling regeneration (Ang et al., 2022; Shinoda and Akasaka, 2020; Tsujino and Matsui, 2022). The present study empirically demonstrated that these stand structural alterations can heterogeneously convert stands from C sink to C source, reducing stored C across landscapes (Fig. 5-5, Fig. 5-8). Assuming that overbrowsing alters stands from PU to SR and CG, it reduces total C stocks by up to 49% and AGC by up to 59% (Fig. 5-5) through the reduction in NPP as

well as increment of HR and SE (Fig. 5-8). In the present study, as discussed below, the lack of renewal trees to compensate for the death of palatable overstory trees was considered to drive stand structural alternations and to be the most dominant factor in FCS degradation.

5.4.2. Possible carbon stock reduction processes

Degradation of understory vegetation due to overbrowsing can impair self-regeneration and recovery in forest ecosystems (Takatsuki 2009). In the present study, NU lost understory vegetation and palatable overstory trees with $D < 10$ cm compared to PU (Table 5-1, Fig. 5-4). Our results are consistent with those of a previous study conducted in the SRF (Enoki et al. 2017). Enoki et al. (2017) reported a reduction in the number of small-diameter trees (i.e., individuals with height > 2 m and DBH < 10 cm) by overbrowsing, from approximately 5900 stems ha^{-1} in 1971 to approximately 1900 stems ha^{-1} in 2013. The stem density of small-diameter trees in NU (palatable trees = 143.8 ± 237.5 stems ha^{-1} , unpalatable trees = 41.5 ± 54.9 stems ha^{-1}) was lower than that reported in 2013 by Enoki et al. (2017). This suggests that overbrowsing continued to reduce the number of small-diameter trees from previous reports (Enoki et al., 2017). Although the AGC in NU did not differ from that in PU at this time, the lack of renewal trees from continued overbrowsing as well as reduced NPP (Fig. 5-8) suggests that AGC would decrease in the future as the canopy tree declines, eventually triggering alterations to SR and CG.

Overbrowsing-induced FCS degradation is expected to be maximized when combined with the loss of overstory trees (Leroux et al., 2020). The present study showed that the reduction in palatable trees led to reductions in AGC and/or NPP in SR and CG (Table 5-2, Table 5-3), agreeing with the predictions of a previous study (Leroux et al., 2020). The increase in unpalatable species and CWD was insufficient to offset the loss of palatable overstory trees in SR and CG. The dominance of unpalatable species, such as Asebi in SR, mitigated the NPP reduction due to the loss of understory vegetation and overstory trees in SR (Table 5-8). Nevertheless, the contribution of Asebi to AGC was negligible in SR (Fig. 5-5). This is because the small size of Asebi (Table 5-1) led to a lower C retention potential as a living biomass. Therefore, the increase in unpalatable species did not compensate for the loss of palatable species. Although CWD mitigated the reduction in AGC in CG (Table 5-2), it increased HR and thus degraded NECB (Fig. 5-8, Fig. S5-12). The residence time of CWD was estimated to be 9.5 years by dividing the C stock of CWD by the HR from CWD. This means that C emissions

from the CG will continue for the next decade, accompanied by AGC reduction without effective conservation measures.

There were no significant differences in BGC between PU and other stand types, whereas there was less leaf litter in NU, SR, and CG and less SOM at 0–10 cm depth in NU and SR than in PU (Table 5-2). There were three possibilities to reduce C stocks in leaf litter and SOM: (1) reductions in leaf litter production (Prescott and Grayston 2023; Deng et al. 2023) and fine root production (Kooijman and Smit, 2001), (2) increased HR from surface litter and SOM (Stark et al. 2000; Metcalfe and Olofsson 2015; Kawakami et al. 2020), and (3) increased SE (Mizuno et al. 2021). The possibility for reductions in leaf litter production and fine root production was denied except for CG because of no reduction of above-ground litter production (Fig. S5-9) and fine root production (Fig. S5-10) in the present study. Similarly, there were only small differences in HR from surface litters and SOM among stand types (Fig. S5-12). Regarding SE, the annual eroded depth was higher for NU, SR, and CG than for PU (Fig. 5-6). Therefore, it is thought that the increased SE was the main cause of the reductions in C stocks of surface litter and SOM at 0–10 cm depth.

Loss of understory vegetation enhances surface litter runoff and SOM detachment through soil erosion (Wakahara et al. 2008; Song et al. 2020). Given that the surface litter mitigates the throughfall kinetic energy of raindrops (Miyata et al. 2019) and, hence, the soil erosion rate (Wakahara et al., 2008), the reduction of surface litter leads to further increases in soil erosion. These imply that conversion from PU to NU enhances SE. Although there was understory coverage of Asebi and moss species in SR and CG, respectively (Fig. S5-4), their distribution was patchy and limited, not covering the entire stand. These suggest that conversion from NU to SR and CG will not be able to mitigate the increment of SE. The inference, as mentioned earlier, is supported by the negative relationships between annual eroded soil depth and C stock in SOM at 0–10 cm depth (Fig. 5-7). In other words, much of SOM had already been flushed away in the severe erosion plots. In summary, although the BGC in NU, SR, and CG did not differ from that in PU at this time, the plant-soil feedback associated with reduced AGC will reduce BGC in the future.

5.4.3. Conclusion

This chapter investigated the impacts of overbrowsing-induced stand structural alteration on FCS. Although the loss of understory vegetation following overbrowsing had a marginal

direct impact on FCS, it spilled over into reductions in other components through ecological processes, such as the lack of renewal trees and accelerated soil erosion. If the alteration from NU to SR and CG is not addressed in addition to the alteration from PU to NU, substantial C losses can occur (Fig. 5-9). To prevent C loss, appropriate measures against overbrowsing, such as fencing and ungulate population management, need to be implemented before structural alterations occur. Overbrowsing may become prevalent in many regions in the future because of the expansion of ungulates caused by human activity (Iijima et al. 2023). This could alter stand structure, especially with the lack of overstory trees, and degrade FCS in areas outside our study area.

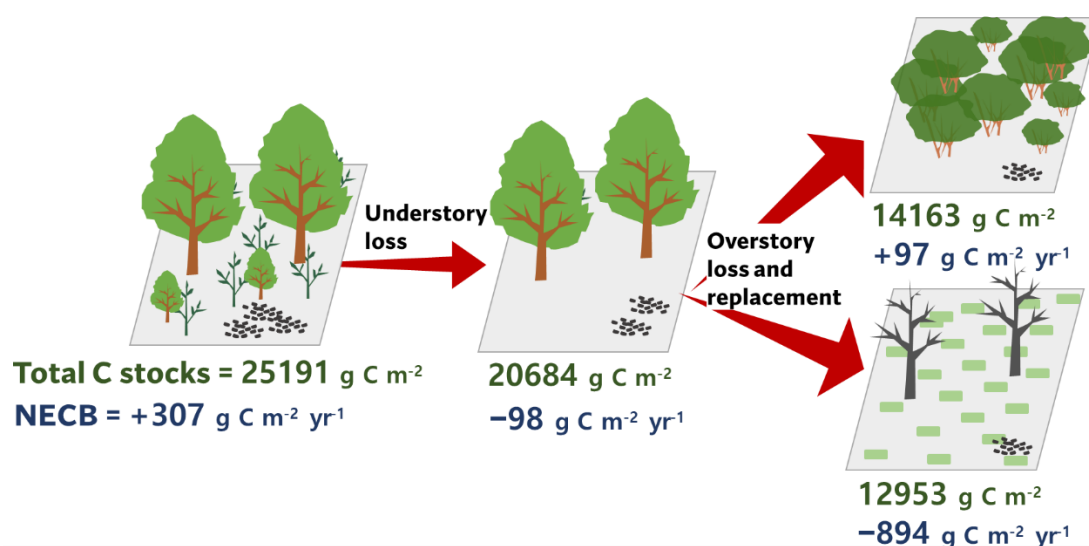


Fig. 5-9. Conceptual diagram of FCS degradation following stand structural alteration in the study area

5.5. Supplemental materials

Table S5-1. The list of species-specific wood gravity (ρ). Tree species are sorted alphabetically by family name.

Family name	Species name	Wood gravity (g cm^{-3})	Reference
Aquifoliaceae	<i>Ilex antisatum</i>	0.605	Umebayashi et al., 2011
Aquifoliaceae	<i>Ilex crenata</i>	0.555	Umebayashi et al., 2011
Aquifoliaceae	<i>Ilex macropoda</i>	0.077	Yazawa, 1941
Araliaceae	<i>Eleutherococcus sciadophylloides</i>	0.426	Komiyama et al., 2011
Araliaceae	<i>Kalopanax pictus</i>	0.467	Umebayashi et al., 2011
Betulaceae	<i>Betula grossa</i>	0.540	Umebayashi et al., 2011
Betulaceae	<i>Carpinus japonica</i>	0.556	Komiyama et al., 2011
Betulaceae	<i>Carpinus laxiflora</i>	0.471	Komiyama et al., 2011
Betulaceae	<i>Carpinus tschonoskii</i>	0.462	Komiyama et al., 2011
Clethraceae	<i>Clethra barbinervis</i>	0.709	Yazawa, 1941
Cornaceae	<i>Cornus controversa</i>	0.468	Komiyama et al., 2011
Ericaceae	<i>Pieris japonica</i>	0.493	Umebayashi et al., 2011
Ericaceae	<i>Rhododendron dilatatum</i>	0.493	Average of Ericaceae family
Euphorbiaceae	<i>Sapinum japonicum</i>	0.521	Umebayashi et al., 2011
Fagaceae	<i>Castanea crenata</i>	0.495	Umebayashi et al., 2011
Fagaceae	<i>Fagus crenata</i>	0.527	Umebayashi et al., 2011
Fagaceae	<i>Quercus acuta</i>	0.961	Nakai and Yamai, 1982
Fagaceae	<i>Quercus crispula</i>	0.594	Umebayashi et al., 2011
Fagaceae	<i>Quercus salicina</i>	0.659	Umebayashi et al., 2011
Hydrangeaceae	<i>Deutzia crenata</i>	0.575	Umebayashi et al., 2011
Hydrangeaceae	<i>Hydrangea scandens</i>	0.575	Average of Hydrangeaceae family
Lauraceae	<i>Lindera erythrocarpa</i>	0.455	Umebayashi et al., 2011
Lauraceae	<i>Lindera triloba</i>	0.516	Umebayashi et al., 2011
Magnoliaceae	<i>Magnolia obovata</i>	0.508	Umebayashi et al., 2011
Pinaceae	<i>Abies firma</i>	0.394	Umebayashi et al., 2011
Pinaceae	<i>Pinus densiflora</i>	0.387	Umebayashi et al., 2011
Pinaceae	<i>Tsuga sieboldii</i>	0.524	Umebayashi et al., 2011

Continued to next page

Table S5-1 (Continued).

Family name	Species name	Wood gravity (g cm ⁻³)	Reference
Rutaceae	<i>Phellodendron amurense</i>	0.408	Umebayashi et al., 2011
Rutaceae	<i>Skimmia japonica</i>	0.408	Average of Rutaceae family
Sabiaceae	<i>Meliosma myriantha</i>	0.671	Yazawa, 1941
Sapindaceae	<i>Acer amoenum</i>	0.536	Average of Acer genus
Sapindaceae	<i>Acer Palmatum</i>	0.525	Umebayashi et al., 2011
Sapindaceae	<i>Acer rufinerve</i>	0.540	Andou et al., 1990
Sapindaceae	<i>Acer sieboldianum</i>	0.544	Umebayashi et al., 2011
Sapindaceae	<i>Acer tenuifolium</i>	0.536	Average of Acer genus
Schisandraceae	<i>Illicium anisatum</i>	0.547	Umebayashi et al., 2011
Styracaceae	<i>Pterostyrax coymbosa</i>	0.430	Umebayashi et al., 2011
Styracaceae	<i>Styrax japonica</i>	0.472	Umebayashi et al., 2011
Symplocaceae	<i>Symplocos lucida</i>	0.495	Umebayashi et al., 2011
Symplocaceae	<i>Symplocos prunifolia</i>	0.495	Average of Symplocaceae family
Theaceae	<i>Stewartia monadelpha</i>	0.610	Umebayashi et al., 2011

Table S5-2. Carbon concentration (g C g⁻¹) of understory vegetation

Growth forms	Carbon concentration (g C g ⁻¹)
Tree seedlings	0.504
Leaf of dwarf bamboo	0.414
Culm of dwarf bamboo	0.441
Moss	0.365
Fern	0.478
Other herbs	0.440

Table S5-3. Carbon concentrations (g C g^{-1}) of leaf litter and fine woody debris (FWD)

Stand types	Litter type	Carbon concentration (g cm^{-3})
Presence understory (PU)	Leaf litter	0.499
	FWD	0.474
No understory (NU)	Leaf litter	0.533
	FWD	0.533
Shrublands (SR)	Leaf litter	0.515
	FWD	0.475
Canopy gaps (CG)	Leaf litter	0.531
	FWD	0.530

Table S5-4. Carbon concentration (g C g^{-1}) of fine roots

Stand types	Carbon concentration (g C g^{-1})
PU	0.439
NU	0.483
SR	0.460
CG	0.484

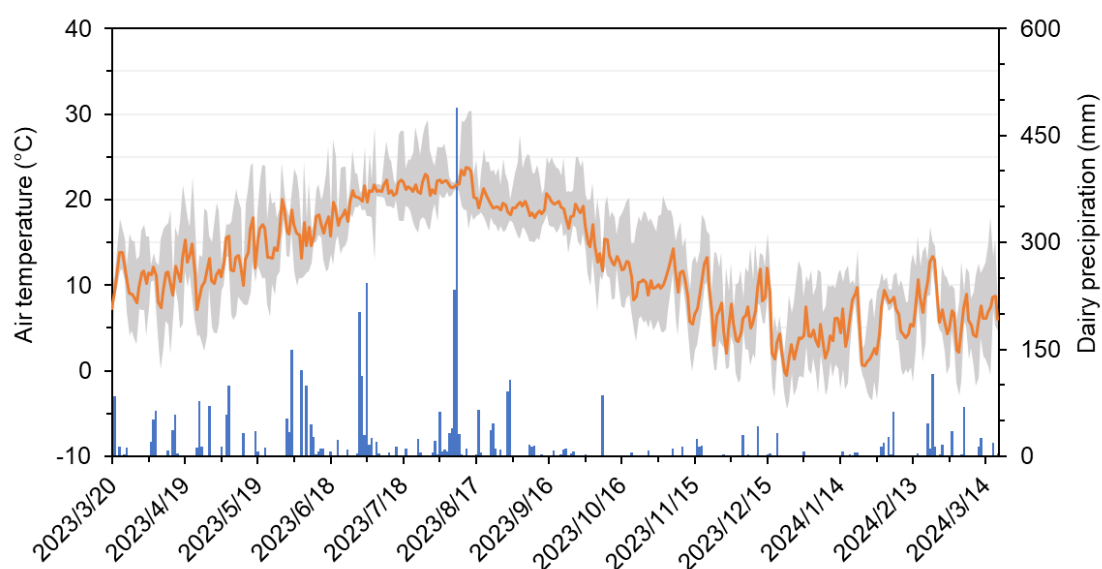


Fig. S5-1. Seasonable variation of air temperature and precipitation in the study area. Orange line indicate daily mean temperature. Shaded area indicates daily maximum and minimum temperature. Blue bars indicate daily total precipitation.

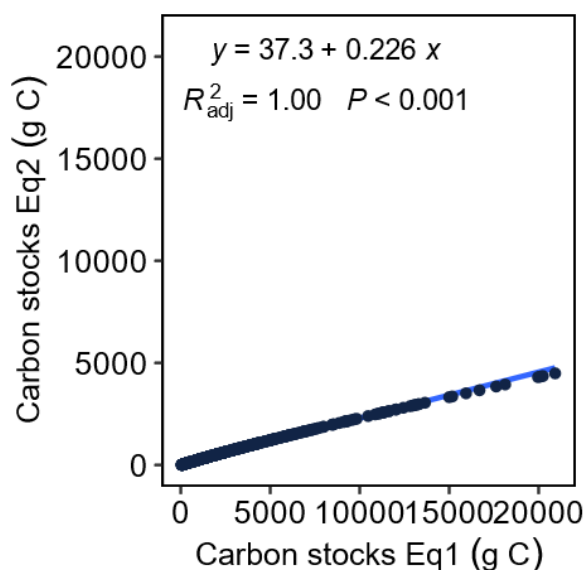


Fig. S5-2. Correlations between individual scale aboveground carbon stock of Asebi (*Pieris japonica*) based on two allometric equations (Eq1; Ishihara et al., 2015, Eq2; Ichihashi and Katayama, 2024).

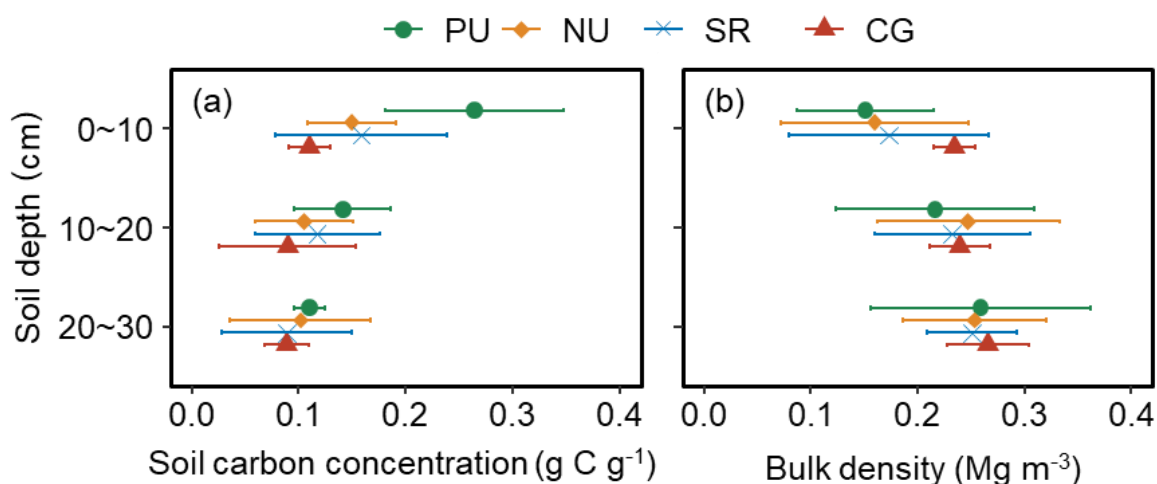


Fig. S5-3. Soil carbon concentration (a) and bulk density (b) at each soil depth. The dots represent the mean value and error bars indicate SD obtained from the plot replicates. Letter * and + indicates $p < 0.05$ and $p < 0.10$ differences to the PU, respectively, based on the two-sided Dunnett tests.

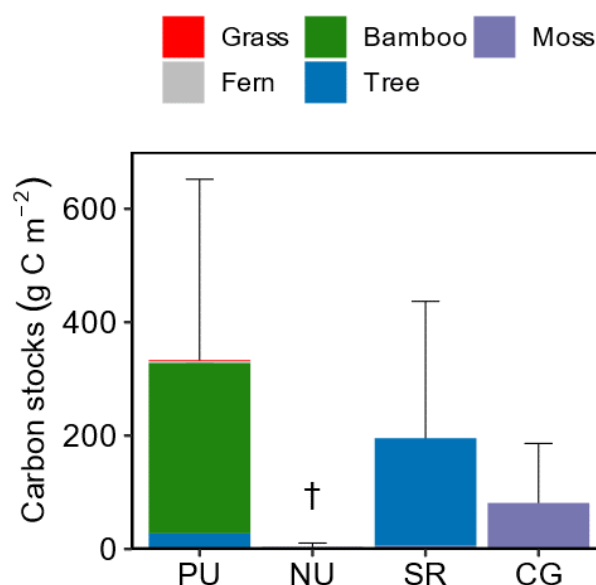


Fig. S5-4. Carbon stock of aboveground understory vegetation by growth forms. The bars indicate the mean value of each growth form. Error bars indicate the SD of the total C stock of understory vegetation. Letter + indicates $p < 0.10$ difference of total C stock of understory vegetation.

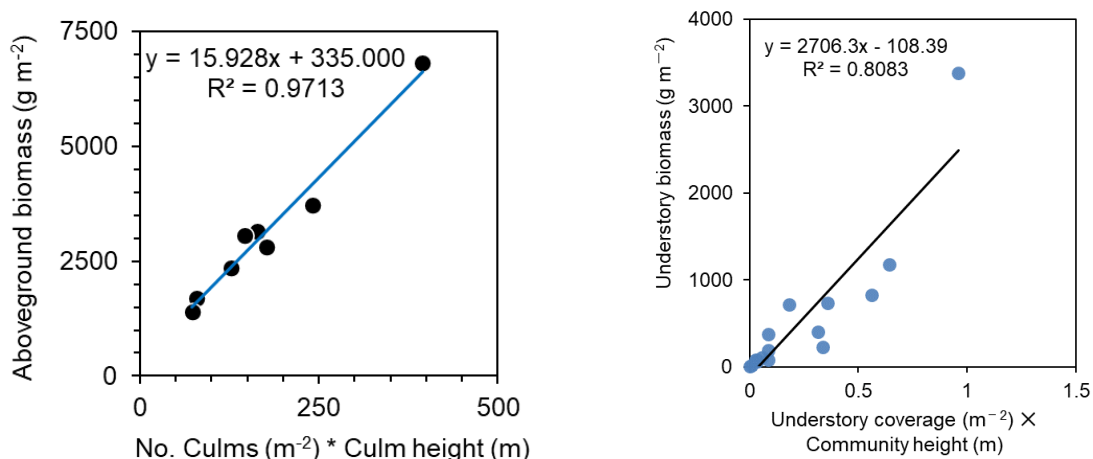


Fig. S5-5. Relationships between aboveground dwarf bamboo (*S. borealis*) biomass and multipliers for culm height and number of culms (left), as well as relationships between understory biomass excluding dwarf bamboo and multipliers for understory coverage and community height (right).

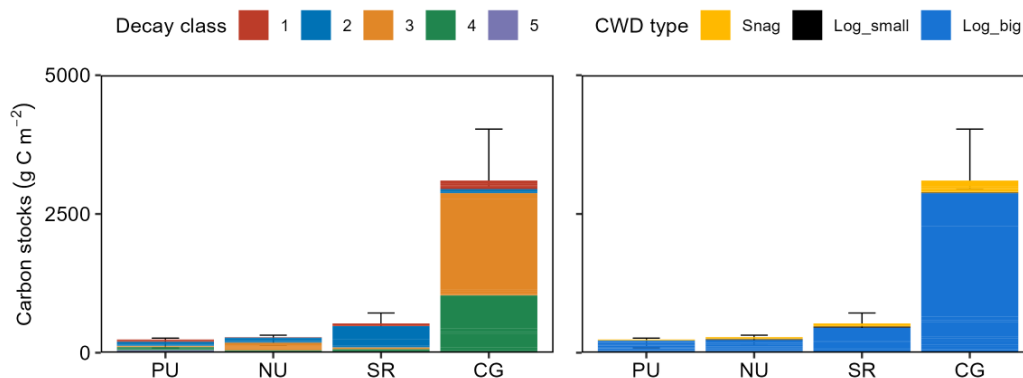


Fig. S5-6. Carbon stock of coarse woody debris (CWD) by decay class (left) and CWD type (right). The bars represent the mean value. Error bars represent SD of total C stock of CWD. Letter + indicates $p < 0.10$ difference of total C stock of CWD from PU based on two-sided Dunnett's test. Note that there were no CWD with decay level 0 in all study plots.

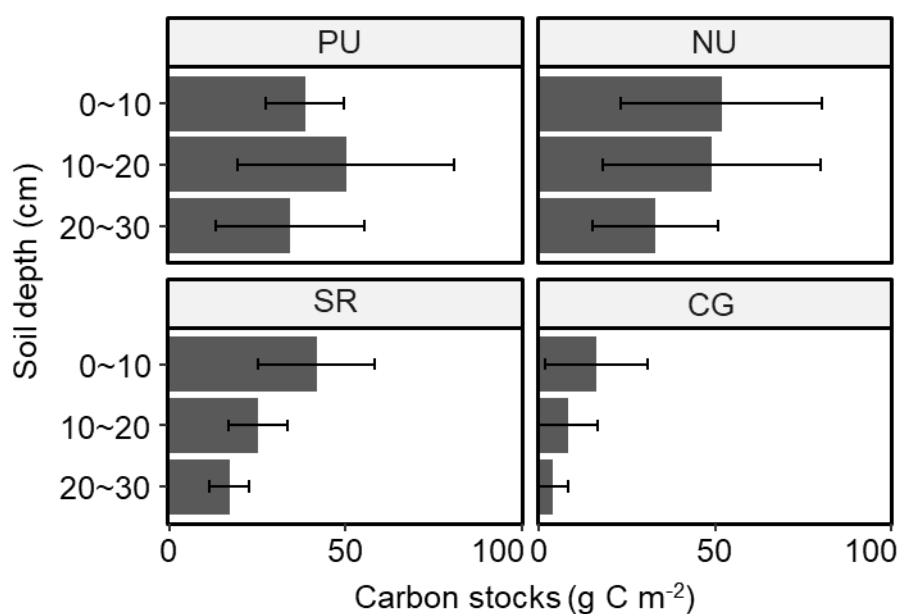


Fig. S5-7. Carbon stocks of fine root in each soil depth layer. The bar represents the mean value, and error bars indicate SD.

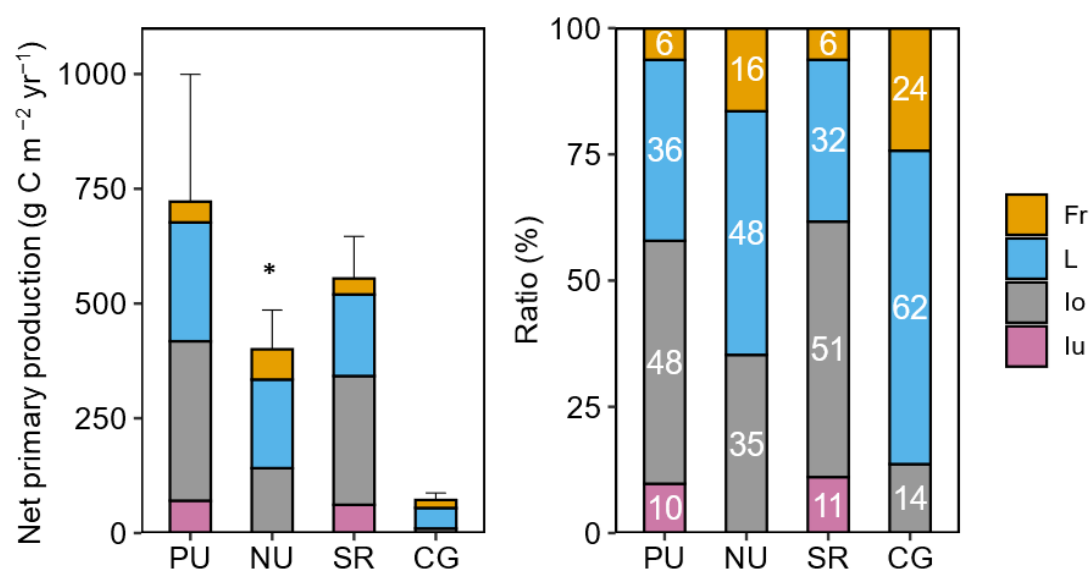


Fig. S5-8. Values of net primary production (NPP) components (left) and its relative contribution (right) in each stand type. In left panel, bars shows the mean value of each component. Error bars indicate the SD of total NPP. Letters * indicates lower P_n from PU with $p < 0.05$ based on one sided Dunnett's test. In right panel, bars shows relative ratio of mean value of NPP components.

Abbreviations for NPP components: F_r ; fine root production, L ; litter production, l_u ; stand biomass increment of understory vegetation, l_o ; stand biomass increment of overstory trees.

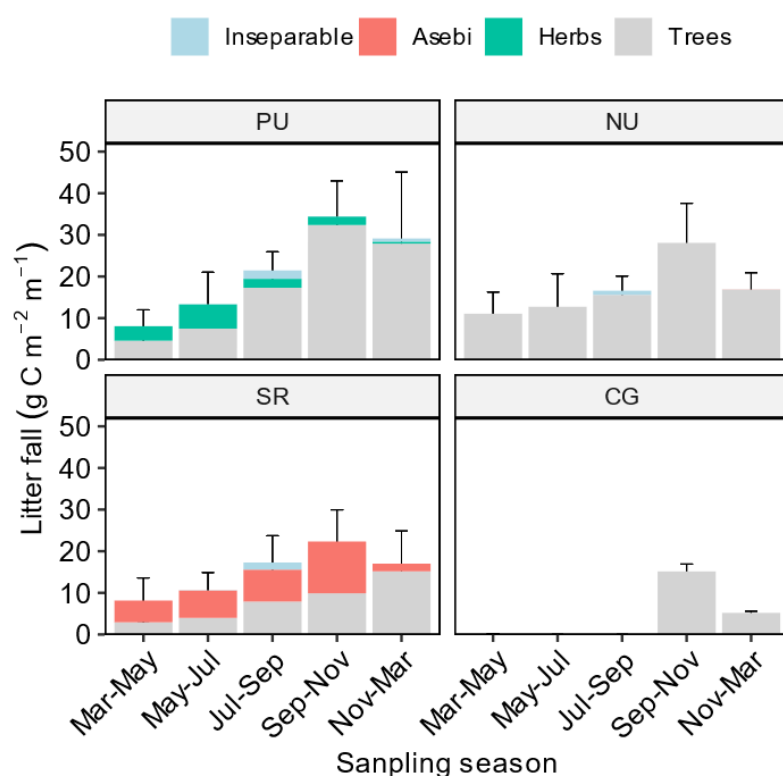


Fig. S5-9. Seasonal changes of litter fall and its species composition for one year from March 2023. The stacking bars indicate the mean value of each species category. Error bar indicates the SD of total litter amount.

Abbreviations for category: IS, litters that have fragmented and become inseparable; Asebi, litters of *P. japonica*; Herbs, litters of understory herb, e.g., dwarf bamboo; Tree, litters of trees except for Asebi. Note that mean and SD of litter fall in CG was calculated from the results of two plots, while other stand types were based on four plots.

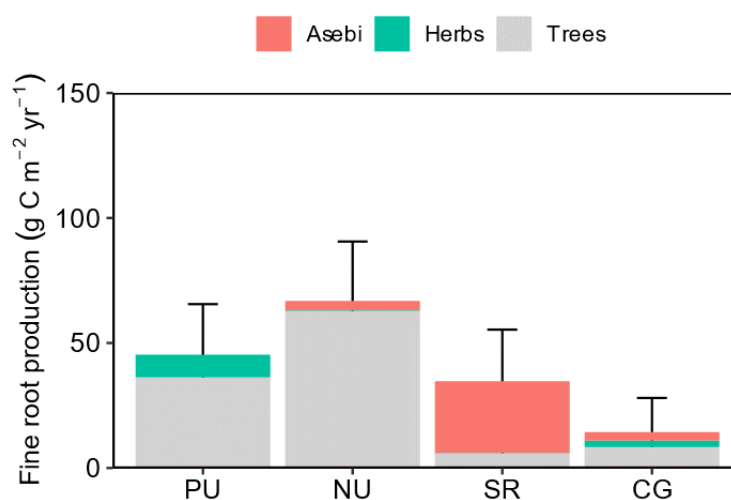


Fig. S5-10. Fine root production and its species composition. The stacking bars indicate the mean value of each species category. Error bar indicates the SD of total fine root production.

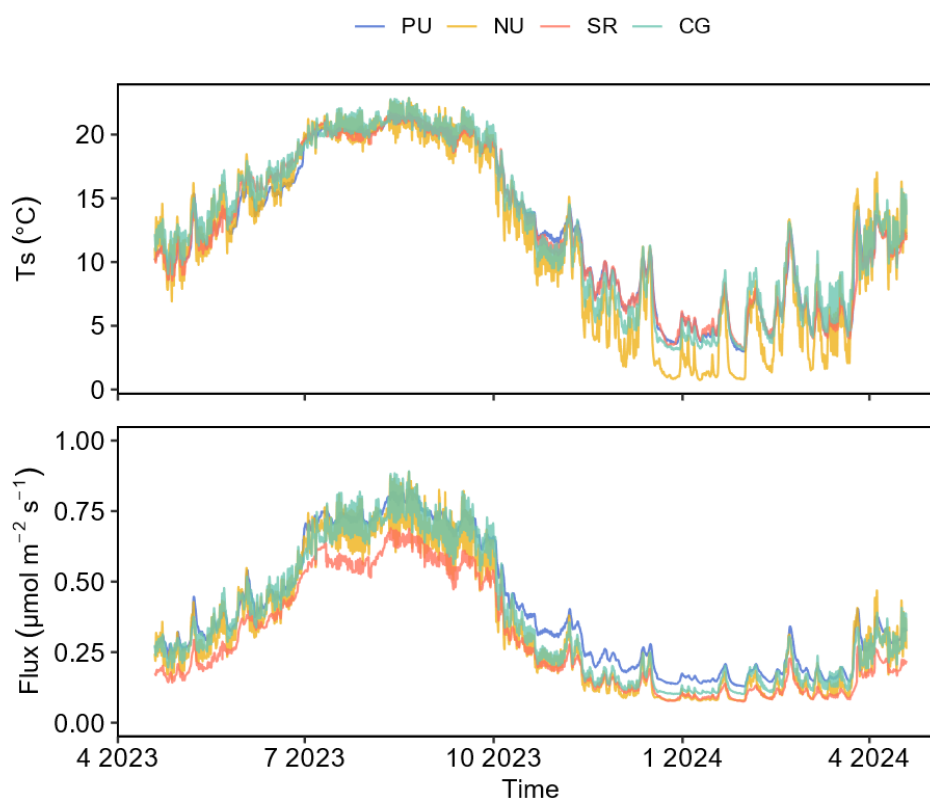


Fig. S5-11. Seasonal changes of soil temperature at 10cm depth (top) and heterotrophic respiration rates from surface litters and SOM for one year from April 19, 2023.

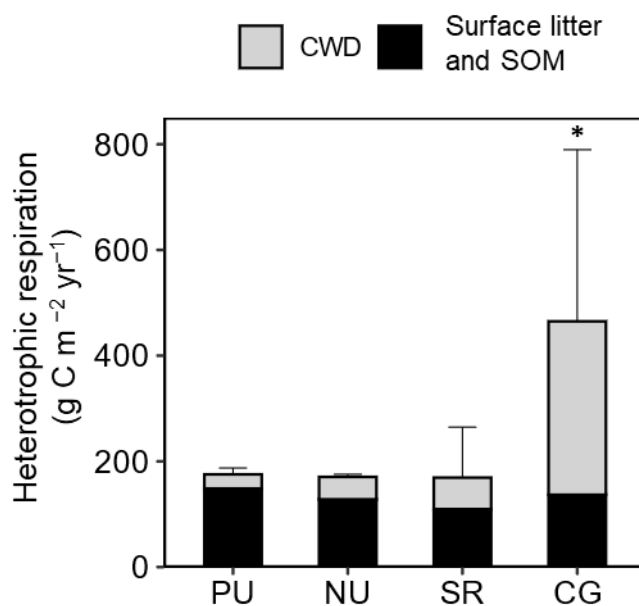


Fig. 5-12. Heterotrophic respiration (HR) of each stand type. The stacking bars indicate the mean value of HR from coarse woody debris (CWD) and HR from surface litters and SOM. Letters * indicates higher Rh from PU with $p < 0.05$ based on one sided Dunnett's test.

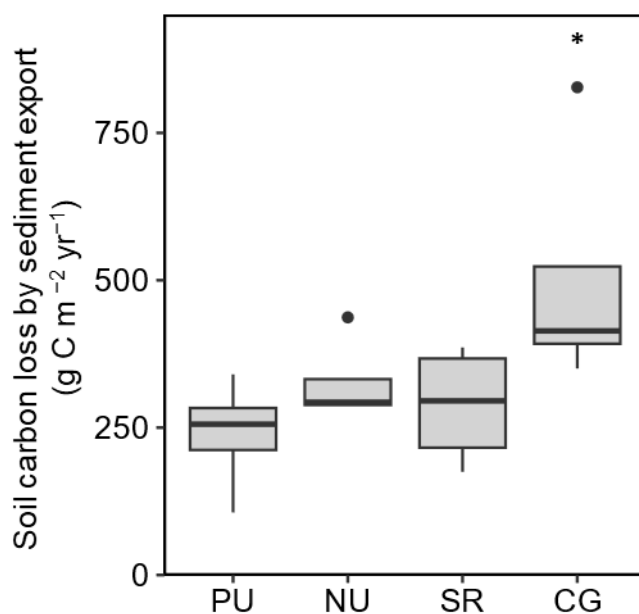


Fig. 5-13. Soil carbon loss from sediment export (SE) of each stand type. Letters * indicates higher Se from PU with $p < 0.05$ based on one sided Dunnett's test.

Chapter 6: Summary and General Discussions

6.1. Brief summary of main findings

Compared to the case of single pulse disturbance (SPLD), there have been limited field studies assessing the impacts of multiple pulse disturbances (MPLD) and press disturbances (PRD) on forest carbon (C) sequestration (FCS). This knowledge gap hinders decision-making regarding the need for countermeasures against MPLD and PRD. It also complicates the development of effective management techniques and the identification of priority areas for management when necessary. In response to this issue, this dissertation targeted two main disturbances: frequent tropical cyclones (TCs) as MPLD and prolonged excessive feeding by sika deer (i.e., overbrowsing) as PRD. The dissertation evaluates their impacts on FCS at the stand-scale. In this evaluation, the dissertation focused on clarifying (1) the extent of FCS degradation, (2) the processes involved in FCS degradation, and (3) the spatial variability of FCS degradation.

Chapters 2 and 3 investigated the effects of frequent TCs on subtropical evergreen broad-leaved forests in the northern part of Okinawa Island. The findings showed that the stem biomass in this forest did not increase due to the high production of coarse woody debris (CWD) resulting from stem breakage and subsequent standing death. Production of CWD is particularly evident in taller trees. Consequently, frequent TCs may limit the increment of canopy height and biomass accumulation in overstory trees. Simultaneously, frequent TCs converted a significant portion of the overstory biomass into CWD, which increased C stocks in dead organic matter (DOM) pools and enhanced heterotrophic respiration (HR) from these pools. By comparing aboveground C stocks (AGC) and net ecosystem production (NEP) in the present study site with intact subtropical forests (Sun and Guan 2014; Yu et al. 2014), it was inferred that frequent TCs reduce AGC slightly (up to 12% reduction, Table 6-1) while reducing NEP extremely (195% reduction, Table 6-2).

Chapters 4 and 5 recorded the impact of prolonged overbrowsing and soil erosion on cool-temperate forests in the southern part of Kyushu Island. Overbrowsing in this area transformed the stand with understory vegetation (PU) into ones with no understory vegetation (NU). The findings indicated that soil erosion has progressed in NU, resulting in the spatially heterogeneous exposure of tree roots. This root exposure further leads to the growth decline of overstory trees through water uptake limitation, possibly accelerating overstory mortality. Tree

decline and death, combined with the lack of recruitments for the original dominant tree species, further altered NU into stands with unpalatable shrub species (SR) and ones with canopy gap areas (CG). These alterations can be assumed to reduce the total C stocks by up to 49% and AGC by up to 59% (Table 6-1). This was due to the up to 391% reduction of net ecosystem C balance (NECB) (Table 6-2), mainly due to the reduced net primary production (NPP), increased HR from CWD, and increased C loss by soil erosion.

Here, this chapter aims to integrate the above-mentioned findings from each chapter. Specifically, this chapter tries to (1) generalize the extent of MPLD and PRD-induced FCS degradation by comparing the case of SPLD, (2) integrate the FCS degradation process with the vegetation re-organization process, and (3) propose the implications of this dissertation in the context of the forest management against spatially heterogeneous disturbances.

6.2. Extent of the forest carbon sequestration degradation

The extent of C stock reductions due to MPLD and PRD was similar to that of SPLD. The extent of C stock reductions due to SPLD depends on whether the stored C was exported from the system (Williams et al. 2016). Specifically, TC and beetle outbreaks may lead to the mortality of living overstory trees, but a significant portion of this biomass remains within the stand as CWD, thereby avoiding drastic reductions in total C stocks and AGC (Williams et al. 2016; Johnstone et al. 2016) (Table 6-1). For example, a single TC has been reported to reduce total C stocks by up to 21% (Davis et al. 2003). Beetle outbreaks have been found to reduce total C stocks by 18% and AGC by 10% (Morehouse et al. 2008). In contrast, disturbances that lead to the export of accumulated C from the system, such as wildfires and landslides, result in significant C stock reduction. Indeed, it has been reported that wildfires reduce total C stocks by up to 98% (Vargas et al. 2008), and landslides reduce it by up to 81% (Schomakers et al. 2019). Regarding MPLD and PRD, this dissertation showed a slight reduction of AGC against frequent TCs (i.e., up to 12% lower AGC compared to the intact forests, Table 6-1). This reduction extent is similar in cases of single TC and insect outbreaks (Table 6-1). In comparison, up to 51% reduction of AGC was estimated due to the prolonged overbrowsing and subsequent soil erosion, similar to the extent of the wildfire and landslide. Although there are limited studies, similar results of C stock reductions have been reported in cases of prolonged drought (i.e., PRD) and frequent snow avalanches (i.e., MPLD). Prolonged droughts have been shown to

have a reduction in AGC limited to 5% (Rigatti et al. 2024). This is because drought-induced dead trees remain in the system as CWD (Huang and Anderegg 2012). In contrast, frequent snow avalanches repeatedly export both tree biomass and SOM, leading to a reported 84% reduction in total C stocks. These findings reveal that the differences in forest C stock reductions across natural disturbances, regardless of temporal characteristics (i.e., SPLD, MPLD, PRD), largely depend on the nature of C movement associated with each disturbance.

Previous studies on SPLD have suggested that C stock reductions due to disturbances tend to be compensated over time. This is because disturbances often lead to a temporary reduction in vegetation biomass while simultaneously promoting the growth of surviving trees and recruitment through seed germination and sprouting. Indeed, most SPLD have initially been reported to cause a temporary reduction in NEP and NECB (Table 6-2) (Bond-Lamberty et al., 2004; Hilton et al., 2011; Satgada et al., 2023; Edburg et al., 2011; Murayama et al., 2024). Subsequently, these metrics experience a magnitude increase, resulting in greater C uptake compared to undisturbed periods within a few decades (Table 6-2). For example, 29 years after wildfires, total C stocks had recovered to levels approximately 34–41% lower than those in intact forests (Vargas et al., 2008). Similarly, 10 years after an insect outbreak, AGC was reported to have recovered to levels just 8% lower than the pre-disturbance state (Hansen, 2014). Conversely, MPLD and PRD lead to more persistent degradation of FCS as long as these disturbances continue or recur. This fundamental difference implies that the reductions in C stocks, as well as NEP and NECB associated with MPLD and PRD, cannot be fully compensated through time alone.

Table 6-1. Examples of carbon stock reductions due to single pulse- (SPLD), multiple pulse-(MPLD), and press- (PRD) disturbances

Agents	Clim ate	Forest type	Period (yr)	Carbon stocks (g C m ⁻²)			%Reduc tion	References
				Target	Baseline	Altered		
SPLD								
Wildfire	T	EB	1	Total C	15600~	420	97~98	Vargas et al., 2007
	T	EB	9		17500	6150	60~64	
	T	EB	29			10260	34~41	
Landslide	ST	EB	6	Total C	29740	5400	81	Schomakers et al., 2019
			41			15610	48	
Insect outbreak	CT	EC	0–2	Total C	24400	22500	18	Morehouse et al., 2008
					AGC	17300	15600	
	CT	EC	10	AGC	8475 ^c	7797 ^c	8	Hansen 2014
29			AGC		8220 ^c	3		
Single TC	CT	DB	10	TGC	19260 ^b	15100	21	Davis et al., 2003
	CT	EC	64	AGC	20218	17353	14	Hotta et al., 2020
MPLD and PRD								
Frequent TCs	ST	EB	<1	AGC ^a	6223~9872 ^b	8684	0~12	This dissertation
Snow avalanches	B	EC	<1	Total C	20100 ^d	3200 ^d	84	Vacchiano et al., 2015
Deer overbrowsing	CT	DB-EC	20~40	Total C	25191	12953~20684	18~49	This dissertation
				AGC	13301	5399~10952	18~51	
Drought	CT	DB	<20	Biomass	9604	6664	31	Huang and Anderegg, 2011
	T	EB	20	Total C	2764 ^c	2634 ^c	5	Rigatti et al., 2024

Abbreviation: T; tropical, ST; sub-tropical, CT; cool-temperate, B; boreal, DB; deciduous broad-leaves, EB; evergreen broad-leaves, and EC; evergreen conifer.

Note that period (yr) indicates times since SPLD and MPLD, as well as the duration of PRD.

Superscript a: AGC was calculated by the sum of stem biomass, surface litter necromass, and CWD necromass.

Superscript b: Values were intact subtropical forests in China calculated from Sun et al. (2014) and Fang et al. (2007).

Superscript c: Values were obtained from the original figures using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). Superscript d: Since authors only reported dry mass, the displayed value was estimated using a fixed C concentration of 0.5 g C g⁻¹.

Table 6-2. Examples of anomaly change of net ecosystem carbon balance (NECB) and net ecosystem carbon production (NEP) due to single pulse- (SPLD), multiple pulse-(MPLD), and press- (PRD) disturbances

Agents	Clim ate	Forest type	Period (yr)	Carbon stocks (g C m ⁻²)			%Change	References
				Target	Baseline	Altered		
SPLD								
Wildfire	B	EC	6	NEP	9 ^{a, b}	-74 ^a	-922	Bond-Lamberty et al., 2004
			20		9 ^{a, b}	310	+3344	
			6		-19 ^b	-136	-615	
			71		-19 ^b	112	+689	
Landslide	CT	EB-EC	40	NECB	37	86	+132	Hilton et al., 2011
	CT	DB-EC	64	NECB	114~382	93~373	-76~+228	Satgada et al., 2023
Insect outbreak	B	EC	5	NEP	17 ^a	-150 ^a	-960	Edburg et al., 2011
			18		37 ^a	-17 ^a	-147	
			32		66 ^a	44 ^a	-34	
Single TC	CT	DB-EC	1	NEP	288 ^c	96	-67	Murayama et al., 2024
			5		288 ^c	252	-13	
			8		288 ^c	444	+54	
MPLD and PRD								
Frequent TCs	ST	EB	<1	NEP	362 ^c	-346	-195	This dissertation
Deer overbrowsing	CT	DB-EC	20~40	NECB	307	-894~97	-391~-68	This dissertation
Drought	T	EB	1	NEP	37	4	-91	Gatti et al., 2014
	CT	DB-EC	5	NEP	214	134	-37	Schwalm et al., 2012

Abbreviation: T; tropical, ST; sub-tropical, CT; cool-temperate, B; boreal, DB; deciduous broad-leaves, EB; evergreen broad-leaves, and EC; evergreen conifer, NECB; net ecosystem carbon balance; NEP; net ecosystem production.

Note that period (yr) indicates times since SPLD and MPLD, as well as the duration of PRD.

Superscript a: Values were obtained from the original figures using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>).

Superscript b: The 151-year-old stand was assumed to be an undisturbed stand.

6.3. Process of forest carbon sequestration degradation: insights from the vegetation reorganization process

The prolonged degradation of FCS caused by MPLD and PRD may be accompanied by the cumulative loss of living vegetation due to increased tree mortality and restricted recruitment with non-resilient reorganization patterns (i.e., restructuring, reassembly, and replacement proposed by Seidl and Turner, 2022). The specific processes obtained through literature and this dissertation are outlined as follows (Fig. 6-1).

Frequent TCs were inferred to cause restructuring, transforming original stands into ones characterized by lower canopy heights and high amounts of CWD (Fig. 6-1a). Except in the case of a catastrophic one that kill all of the trees in a stand, TCs generally cause growth reduction due to defoliation and stem breakage (Ackerman et al. 1991; Everham and Brokaw 1996). These impacts temporarily convert stands into the transitional state as open-canopy stands (Fernandez and Fetcher 1991; Lin et al. 2003; Turton and Alamgir 2015). If no subsequent TC occurs, the open canopy rapidly re-closes (i.e., resilience) through the regrowth of broken individuals, resprouting from damaged trees, and growth release of residual trees due to reduced competition (Everham and Brokaw 1996; Bellingham et al. 1996; Lin et al. 2011). Most researchers suggest that this resilience process starts within a few months (Fernandez and Fetcher 1991; Higo 1994; Lin et al. 2018; Abbas et al. 2020). As a result, a single TC generally increases the dominance of pre-existing species in the original stand (Lawton and Putz 1988; Putz and Sharitz 1991; Scatena and Lugo 1995; Dallmeier et al. 1998). In contrast, if TCs occur repeatedly, the regenerated canopy will suffer TC-induced damages again. When stem breakage and tree mortality from repeated TCs outpace canopy regeneration, the stand transitions to an altered state, such as a stand with lower canopy height and abundant CWD. Furthermore, the cumulative growth stress caused by frequent TCs generates more standing dead trees, facilitating such structural alterations and related NEP degradation.

Prolonged overbrowsing can be inferred to cause a replacement process where PU transitioned through NU into SR and CG (Fig. 6-1b). Generally, the primary effects of overbrowsing on stands include reductions in understory vegetation, particularly a decline in seedlings of highly palatable species (Gill 1992; Akashi and Nakashizuka 1999; Takatsuki 2009; Lilleeng et al. 2016). As a result, disturbed stands were temporarily converted into a transitional state as NU. If browsing pressure decreases, e.g., along with a reduction in deer

food resources, the understory vegetation is expected to recover quickly through recruitment from surrounding areas (i.e., resilience from NU to PU). This expectation is supported by many previous studies that observed the recovery of understory vegetation due to installing deer exclosure fences (Smith et al. 2020; Iijima and Oka 2023). However, since Japanese deer's diet is highly flexible, it is unlikely that foraging pressure will decrease immediately, even as food resources become scarce (Oka et al. 2022; Suzuki 2024). Consequently, prolonged overbrowsing may lead to a gradual loss of both living vegetation biomass and recruitment sources in the forest (Gill 1992; Hester 2000; Wright et al. 2012; Beauchamp et al. 2013; DiTommaso et al. 2014; Shinoda and Akasaka 2020). When the recruitment of original vegetation fails due to overbrowsing and cannot keep pace with tree mortality, the forest stand transitions to an alternative state such as SR or CG. Previous studies on deer impacts have suggested that this non-resilient reorganization process usually requires extended periods unless additional natural disturbances, such as beetle outbreaks and landslides (Stromayer and Warren 1997; Kramer et al. 2003; Leroux et al. 2020; Dobor et al. 2024). This dissertation demonstrated that soil erosion resulting from the loss of understory vegetation leads to tree decline and subsequent mortality (details are provided in chapter 4). This implies that deer overbrowsing triggers soil erosion, accelerating tree decline and mortality, thereby hastening the transition from NU to SR or CG with degradation of forest C stocks and NECB.

The timescale required for above-mentioned vegetation reorganization process can be inferred from both the vegetation recovery and turnover time (see supplemental section S.1.3 in chapter 1 for details). Based on tree biomass measurements, the vegetation recovery time in YF area against frequent TCs was estimated to be 0.74–0.99 years (calculated as CWD production ÷ amount of stem growth, using data from 2013–2016 and 2016–2019), whereas the turnover time was estimated to be 46–66 years (calculated as stem biomass ÷ CWD production). In contrast, the return interval of TCs—0.2, which is obtained from the inverse of the annual average TCs frequency between 2010–2019—is much shorter. If the return interval were longer than the vegetation recovery time, TCs at this site could potentially be affected as SPLD. Conversely, if the return interval will be increased in the future and persist for a period exceeding the vegetation turnover time (i.e., 46–66 years), such TCs can behave to influence PRD-like impact, promoting vegetation reassembly or replacement to the system (see section 1.3.2. and S.1.3.). In SRF under the influence of deer overbrowsing, the vegetation turnover time can be estimated as 44 ± 16 years for PU when assuming the growth and death of overstory

trees are in balance (i.e., biomass $\div$ annual growth of overstory trees). Because deer overbrowsing has persisted for more than 40 years at the study site (Saruki et al., 2004), it appears to be at a critical threshold where a shift from PU to SR or CG is imminent. Moreover, heightened soil erosion in the study area has further accelerated ecological changes. Note that these calculations are based on limited information and may not fully capture the complexity of real-world conditions. Moving forward, more accurate examination focusing vegetation recovery and turnover time—along with efforts to distinguish the impacts of various disturbances from other contributing factors—are needed to deepen our understanding of these dynamics.

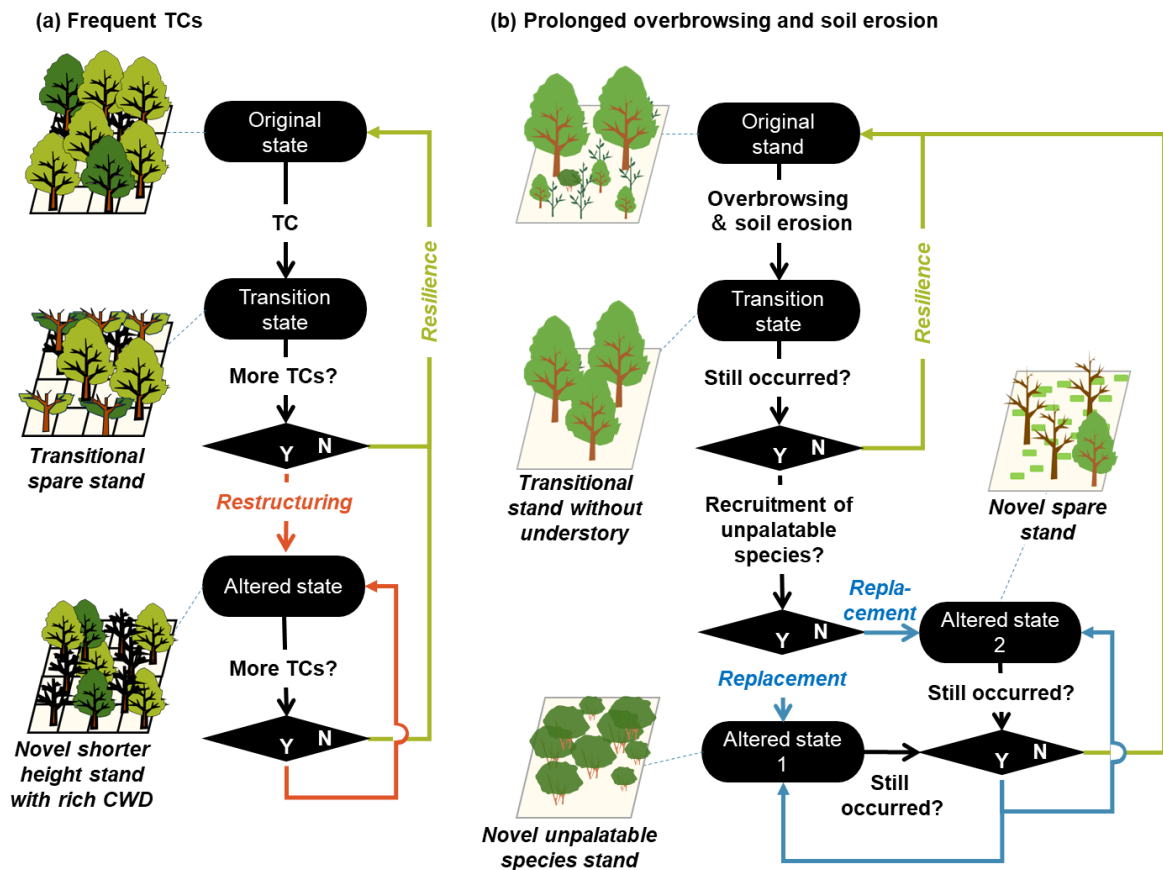


Fig. 6-1. Conceptual diagram of timelines for state transitions in the forest ecosystem against frequent TCs (a) and prolonged overbrowsing and soil erosion (b). Arrows from the branch nodes (diamonds) indicate conditional outcomes (yes = Y, no = N).

6.4. Implication for conservation of forest carbon sequestration

This dissertation quantified the extent of FCS degradation, supporting the conceptual predictions proposed in previous literature (Paine et al. 1998; Flores et al. 2020; Burton et al. 2020; Albrich et al. 2020; Sturtevant and Fortin 2021). Without quantitatively assessing the extent of FCS degradation, it is impossible to fully understand the severity of potential future risks or justify the necessary costs of intervention (Tubiello et al. 2021; Koch et al. 2021; Pan et al. 2024). Furthermore, by clarifying which C components contribute to FCS degradation and identifying the processes involved (e.g., soil erosion and CWD production), this dissertation facilitates the development of targeted intervention measures. Such insights not only help determine whether intervention is needed but also inform evaluations of management cost-effectiveness and the appropriate scope of implementation. The specific findings for the study sites examined in this dissertation are as follows.

This dissertation reveals that frequent TCs cause spatially heterogeneous stem breakage and subsequent tree mortality at the individual tree level, degrading FCS. The northern part of Okinawa Island, the study area, is a biodiversity hotspot in Japan (Itô et al. 2000; Ohsawa et al. 2018). For this reason, most of this area has been registered as a natural World Heritage site (<https://whc.unesco.org/en/list/1574>), and human intervention is restricted. Therefore, there is currently limited potential for co-benefits of biodiversity and FCS in this area; hence activate forest management is required if FCS is to be enhanced. In addition, balancing regional forest conservation with timber production is a key challenge in non-restricted areas (Itô et al. 2000; Kubota et al. 2005; Konoshima and Yoshimoto 2019). For example, the government promotes selective logging rather than clear-cutting (Okinawa Prefectural Office 2018). However, little discussion has been on the optimal approach to selecting trees for selective logging. The findings of this dissertation suggest that prioritizing selective logging for individuals of low-wood-density species, emergent trees, and those with stem breakage could achieve timber production while reducing C losses due to TCs. Additionally, salvage logging, which involves collecting CWD produced by TCs, is a typical post-TC management strategy (Hotta et al. 2020, 2023). Properly implementing salvage logging in a TC-prone environment could compensate for the required timber production. Although this may enhance the reduction of C stocks in disturbed stands, it could help maintain FCS at the landscape level by preserving other stands

from human-induced logging.

Prolonged deer overbrowsing and soil erosion drastically degraded FCS by transitioning PU to SR and CG. Therefore, preventing such transition is crucial to conserve FCS. Transition from PU to SR and CG occurs due to the combination of understory loss and overstory tree mortality. Hence, protecting overstory trees may be essential way to mitigate FCS degradation through maintaining the original canopy tree community as seed producers (Allen et al. 2023; Dobor et al. 2024). Indeed, installing deer exclusion fences has been reported to protect understory vegetation and reduce soil erosion and associated root exposure, consequently sustaining tree growth (Abe et al. 2024). Similarly, erosion control measures, such as installing wooden horizontal steps and ground net covers, could prevent root exposure-induced tree decline (Sun et al. 2020). Such efforts may be more effective if they are prioritized for individuals with pronounced root exposure or individuals that are vulnerable to root exposure (Abe et al. 2022). From this perspective, it will be necessary in the future to compare the exposure of the roots of various tree species and the susceptibility of tree decline, exploring the factors that cause vulnerability. Although it is challenging to implement such vegetation protection and soil erosion control measures across the entire forest landscape, implementing them in small, scattered areas surrounding vulnerable trees, could help sustain overstory tree community within the landscape. This would contribute to future seed dispersal from these areas (Allen et al. 2023; Dobor et al. 2024).

This dissertation focused on disturbance effects at the stand scale and did not evaluate the spatiotemporal heterogeneity of disturbance impacts across the broader landscape. The ways in which disturbances shape landscape mosaics may vary depending on the disturbance type (see the description on S.1.3. in chapter 1). Findings of this dissertation suggest that stand structure may serve as a key indicator of FCS. In addition to visual census (e.g., Saruki et al., 2004), remote sensing technologies could allow us to monitor temporal changes in stand structure over large areas, clarifying landscape mosaic creation patterns and the spatial extent of the FCS degradation (Uden et al. 2019). This approach would also facilitate the identification of critical zones that are particularly vulnerable to specific disturbances. Acquiring this information represents an essential next step for evaluating the necessity and effectiveness of forest management strategies and interventions discussed in this section.

6.5. Limitations and Future Perspectives

The findings of this dissertation were derived from two study sites, each with specific ecological, geological, and meteorological contexts. For example, the study site in chapters 2 and 3 was located on areas mainly covered ridgeline, while less covered valley. Chapter 4 only targeted growth of mature beech trees. Chapter 5 reflected the FCS degradation in areas with promoted soil erosion due to high precipitation. Therefore, while the processes and mechanisms identified in this dissertation offer valuable insights, the extent of their generalizability should be considered such site-specific factors. To further generalize these insights, however, additional investigations under diverse spatial and temporal settings are crucial. Applying similar measurements of FCS across varied meteorology, topography, forest type, and disturbance regime will help clarify which processes are broadly universal and which are unique to specific landscapes.

The TCs and overbrowsing are independent phenomena, but this dissertation did not examine their interactions. A concern has been raised in Okinawa about the introduction of deer (<https://www.okinawatimes.co.jp/articles/-/1458779>) and the increasing population of goats (Takahashi and Tisdell 1992). In addition, TCs regularly approach southern Kyushu (Saito, 2002). Moreover, these disturbances may also interact with other disturbances, such as landslides (Mitsuda et al. 2000; Kimura et al. 2010) and beetle outbreaks (Kotaka et al. 2021; Yamauchi et al. 2022). Given that such interactions among multiple types of disturbances could further degrade FCS (Grimbacher and Stork 2009), future research should focus on understanding the degree and mechanisms of FCS degradation due to various disturbance interactions.

In recent years, knowledge of SPLD on FCS has been considered in ecosystem process models and terrestrial C cycle models (Liu et al. 2011). These models, along with remote sensing, have been employed to estimate the impact of SPLD on FCS globally (Pugh et al. 2019). For example, Roebroek et al. (2023) estimated that the potential carbon stocks of overstory trees could reach 400 Pg C, whereas the observed carbon stocks of overstory trees remain at only 150 Pg C. This discrepancy has been attributed to the effects of natural disturbances (Pugh et al. 2019; Roebroek et al. 2023; Pan et al. 2024). In contrast, the impacts of MPLD and PRD have yet to be considered in such analyses (Seidl et al. 2011; Buma 2015; Williams et al. 2016; Sturtevant and Fortin 2021). Since the findings of this dissertation are based on stand-scale observations, it is necessary to generalize these findings and scale them

up to landscape or regional levels in future research. Specifically, the development of ecosystem process models explicitly incorporating MPLD and PRD. In addition, combining these models with the spatial data of vegetation distribution could provide a more comprehensive understanding of FCS dynamics at the landscape level. Such efforts would also enable deeper insights into the effects of various disturbance interactions, as well as the impacts of different disturbance scales, which are challenging to capture through observational studies alone.

6.6. Concluding remarks

This dissertation demonstrated that MPLD and PRD lead to tree decline and mortality, which in turn reduce NPP as well as increase HR from CWD and C loss through soil erosion. Consequently, these decrease NEP or NECB, limiting or decreasing forest C stocks in stands. While the extent of FCS degradation via MPLD and PRD is similar to that via SPLD, MPLD, and PRD are expected to cause more persistent FCS degradation, possibly accompanied by the non-resilient vegetation reorganization process, as long as disturbances continue. Although these findings are based on specific disturbance drivers, locations, and timeframes, they provide empirical evidence that increased frequency and persistence of natural disturbances could convert present forests or newly planted forests, which are expected to serve as C sinks, into sustained C sources. Therefore, assessing FCS across various forests and promptly implementing mitigation measures in severely affected areas will be crucial.

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