

**Photosynthesis Properties of Pioneer Species on
Volcanically Devastated Sites in Miyake-jima Island,
Japan**

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Japan**

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1. General Introduction

1.1. Background of the research

Volcanic eruptions are powerful agents of large infrequent disturbances and create exemplary living laboratories that can be used to investigate both initial disturbance effects on ecosystems and longer-term successional processes (del Moral and Grishin 1999). Primary succession often occurs following the complete destruction of a biosystem where the ground surface is covered by rocks and/or inorganic materials (del Moral and Bliss 1993; Tsuyuzaki 1995; Vitousek and Walker 1987; Vitousek et al. 1989). Researchers have conducted a series of studies to explore what controls, constrains, or promotes the vegetation development in such harsh habitats (Walker and del Moral 2003) by exploring the importance of microsites (Wood and del Moral 1987), mycorrhizae (Titus and del Moral 1998), biotic interactions (del Moral and Rozzell 2005), and dispersal (Fuller and del Moral 2003; del Moral and Eckert 2005). Many ecological studies of successional changes in species composition, biomass, growth form, leaf size, leaf shape, and canopy arrangement have been conducted following volcanic eruption (e.g., the volcano Mount St. Helens in the USA (del Moral Wood 1993; Wright et al. 2001; Weber et al. 2006) and Mt. Usu (Haruki and Tsuyuzaki 2001); and Miyake-jima volcanic island (Kamijo et al. 2002; Kamijo and Hashiba 2003) in Japan). However, most of the studies were conducted using the insight of the population and community (Mooney and Godron 1983; White 1985; Huston 1994). Few studies have focused on the physiological ecology of species living in such a harsh habitat, which is important for revealing the mechanism of succession and is important for the restoration of the local ecosystem.

1.2. Environmental feedback

The initiation of any succession depends on the initiating disturbance, after which environmental and landscape factors come into play. Stress is the major factor that governs successional rates. Grime (1977) defined stress as any external constraint that limits the rate of dry matter production of all or part of the vegetation. Once plant species commence their invasion, a process strongly affected by landscape factors, conditions normally start to ameliorate, and interaction with the local environment commences. Any environmental factor that affects the rate of biomass accumulation will affect the rate of succession.

The environment of a plant may vary daily, seasonally, vertically, and horizontally. The level of variability is determined by many factors, including climate, geographical location, geomorphological features, the nature of site disturbances, and the number and type of species present. The influence of the environment on the plant depends not only on the level of environmental variability and the predictability of that variation but also on the change in physiology over time. Changes in plant species composition during primary succession are interpreted as reflecting gradients from the high-light and low-nutrient conditions occurring early in the succession to the low-light and high-nutrient conditions occurring later on (Tilman 1982, 1986; Vitousek et al. 1989). The environmental variability in open, early successional habitats is generally thought to be higher than that in closed, late-successional habitats. In the early stage of succession, stresses including infertility and drought (Kardol et al. 2010) severely constrain the vegetation recovery process.

1.2.1. Changes in soil nutrient content

Nitrogen (N) and phosphorus (P) are the nutrients that most frequently limit primary productivity in terrestrial ecosystems (Vitousek and Howarth 1991; Elser et al.

2007). Overall, plant growth in ecosystems with young soils might generally be expected to be N-limited, whereas growth on older soils should be P-limited; in intermediate-aged sites N and P equilibrate at higher supply levels (Walker and Syers 1976).

In the early stages of volcanic primary succession, nitrogen is often the most limiting resource (Vitousek and Howarth 1991; Elser et al. 2007). Unlike other nutrients that can be released through weathering of the underlying rock, nitrogen must either be transported to primary successions through leaching and deposition or fixed in situ. The soil nitrogen content varies greatly at different stages of succession. Plant growth during this stage is severely limited by soil N content. The limitation of N is more serious to early pioneer species than it is to later species (Huante et al. 1995; Fetcher et al. 1996). In general, the difference in nutrient content among soils at the same site is often due to the different types of disturbance, the disturbance severity and the initial conditions (Vitousek and Sanford 1986; Uhl and Jordan 1984; Uhl 1987).

1.2.2. Changes in light conditions

During the succession, light is also an important ecological factor that affects plant growth, survival and distribution (Messier and Puttonen 1995; Veneklaas and Oudena 2005; Wyka et al. 2007; Jensen et al. 2012). The variability of the physical environment is related primarily to the amount of energy that reaches the soil surface and the way in which it is dispersed from the surface. In the early-stage successional habitat, due to the lack of vegetation coverage, plants grow in an open environment with full sunlight. The total amount of radiation above the community varies only minimally. Energy exchange occurs at or near the soil surface, where maximum temperature fluctuations occur, and light energy reaches the surface unaltered. In the later successional stage habitat, the

surface of energy exchange is the upper layers of the canopy. The presence of plant canopies results in a low quantity and quality of light, thereby severely limiting the growth and survival of understory plants (Givnish 1988; Messier et al. 1999; Robakowski et al. 2003; Zhang et al. 2003; Veneklaas and Oudena 2005). Temperature fluctuations below the canopy are buffered by the vegetation itself, and progressively less energy penetrates toward the forest floor; the light that does reach the floor is markedly depleted of photosynthetically active wavelengths. Thus, plant growth in the understory during the late successional stage, except in areas of large light gaps, experience a less variable and less extreme environment in the forest with respect to temperature, humidity, and wind. Sunflecks under a canopy result in extremely variable light intensity and possible rapid fluctuation of leaf temperature.

Although the relationships between species and habitat environment have been well clarified for plants grown in constant or controlled environments (Vitousek et al. 1993; Ellsworth et al. 1996; Sun et al. 2016), we know considerably less about such relationships in natural volcanic environments.

1.3. Ecophysiological characteristics of pioneer species after volcanic disturbance

After volcanic eruptions, the damaged vegetation ecosystem begins to enter the recovery phase. The different disturbance severity, and the high heterogeneity of habitats require the vegetation to have distinctive physiological characteristics to adapt to these different habitats. For example, species that successfully colonize bare land generally have physiological or ecological characteristics that are well-adapted to harsh environments and are more tolerant to drought and nutrient stress (del Moral and Wood 1993). Among the countless plant species, pioneer species are undoubtedly the best choice for such conditions. Several studies have shown that pioneer plant species can

have a large effect on the entire local ecosystem by influencing the input of nitrogen by biological fixation (Vitousek and Walker 1987; Hughes and Denslow 2005), rates of biogeochemical processes (Ehrenfeld 2003), decomposition and mineralization rates of plant litter (Ehrenfeld et al. 2001; Standish et al. 2004), and stock of nutrients in the soil (Hughes and Denslow 2005). Thus, these effects of pioneer species should be most pronounced when they differ in N-fixing ability and photosynthetic pathway (e.g., C₃, C₄).

Leaf nitrogen (N) content (N_{area}), dark respiration rate (R_d), and photosynthetic capacity (A_{max} , photosynthesis under saturating light) are the core leaf economics traits (Wright et al. 2004). Efficient use of these N is believed to contribute to plant fitness (Aerts and Chapin 1999) and is thought to influence the N cycling and productivity of local ecosystems (Vitousek 2004). The net photosynthesis rate accomplished per unit N, termed photosynthetic N-use efficiency (PNUE), has been considered an important plant functional trait to characterize species in relation to their leaf economics, physiology, and strategy (see Hikosaka 2004 for review). These leaf traits and trait relationships have been well studied on a global scale. However, these growth strategy-related leaf traits for pioneer species in volcanically devastated sites are not well understood. At the leaf level, there is a very strong correlation between A_{max} and N_{area} (e.g., Field and Mooney 1986; Sage and Percy 1987; Anten et al. 1995). However, the A_{max} achieved at a given N_{area} (PNUE) is not the same for all plants (Field and Mooney 1986). In particular, more complete knowledge of PNUE for pioneer species differing in N-fixing ability and photosynthesis pathway, is critical to ecological explanations of succession mechanisms and functions of the volcanic ecosystem.

Colonization of new soils by N-fixing plant species results in greatly improved ecosystem process rates, soil fertility, and nutrition of the co-occurring non-N-fixing

plant species (Vitousek et al. 1987; Hooper and Vitousek 1998). Furthermore, N-fixing species often have higher leaf nutrient concentrations (Cornelissen et al. 1997; Peltzer et al. 2009) and low LMA (Craine et al. 2002; Wright et al. 2004; Tjoelker et al. 2005) when compared to those of non-N-fixing species. These traits can be associated with higher rates of litter decomposition (Knops et al. 2002; Tatenos et al. 2007). As for non-N-fixing species differing in photosynthetic pathway, species possessing the C₄ photosynthetic pathway are generally found to have higher PNUE than that of those with the C₃ photosynthetic pathway (e.g., Sage and Pearcy 1987; Anten et al. 1995). These trait differences, in turn, have functional consequences. If these key traits of pioneer species do indeed differ in N-fixing ability and photosynthetic pathway, then the impacts of these pioneer species on ecological processes could potentially be predicted from their N-fixing ability and photosynthetic pathway.

1.4. Restoration using pioneer species

Successful ecosystem restoration requires a fundamental understanding of the ecological characteristics of the component species, combined with knowledge of how they assemble, interact and function as communities (Pywell and Putwain 1996). There is increasing interest in using species traits, as well as the grouping of species into functional types using their traits, to both predict plant community responses to environmental change and to address the mechanisms underlying these responses (Lavorel et al. 1997; Weiher et al. 1999). The importance of pioneer species in restoring local ecology has long attracted the attention of many researchers. Owing to their respective advantages in persisting the extreme local environmental conditions, native pioneer species are important candidates for restoring local ecology. Furthermore, in volcanically devastated sites, combined with some revegetation technology, local

environment restoration using native pioneer species has resulted in rapid development (Vitousek and Walker 1989; del Moral and Grishin 1999). The advantages of using native pioneer species as candidates for ecological restoration have been well clarified. However, the fundamental knowledge of the advantages of leaf physiological traits remains unclear.

1.5. Purpose of research

The Miyake-jima Island is an active volcano in Japan. Historically, there have been many eruptions, the most recent of which occurred in 2000 (Kamijo and Hashiba 2003). After this eruption, the vegetation was severely damaged by the substantial amount of volcanic ash, and extensive bare land was formed around the volcanic crater. As the distance from the crater increased, the extent of the damage was progressively reduced. On the volcanically devastated sites of Miyake-jima Island, representative pioneer species, such as *Miscanthus condensatus*, *Alnus sieboldiana* and *Fallopia japonica* var. *hachidyoensis*, have successfully invaded and established, with *M. condensatus* as the most dominant species. These three pioneer species differed in their N-fixing ability and photosynthetic pathway.

The current research on the photosynthetic properties of pioneer species in volcanically devastated sites with poor nutrient condition has been conducted in Hawaii (Cordell et al. 2001), Mt. Fuji (Sakata et al. 2006), and Miyake-jima Island (Choi et al. 2014). Choi et al. (2014) focuses on *Alnus sieboldiana*, an N-fixing pioneer tree species, and examined the response of photosynthetic properties to the concentration of volcanic gas. However, only a few studies have suggested the effects of different habitat conditions (mainly light and low-nutrient soil conditions) on the photosynthetic characteristics, leaf structure parameters, and biochemical parameters (leaf nitrogen) of

the pioneer species in volcanic succession. In addition, there have been no physiological studies of *M.condensatus* in volcanically devastated sites, despite its ecological importance in volcanic succession.

In this study, I concentrate on the physiological adaptations of pioneer species to environmental variability. To evaluate the photosynthetic properties of pioneer species in volcanically devastated sites, I conducted a series of studies as follows:

- 1) As *M. condensatus* on Miyake-jima Island has been the absolutely dominant species following the eruption in 2000, to conserve the native ecosystem, the Tokyo Metropolitan Government plans to use native species in the revegetation program. *M. condensatus* is a candidate plant for the program because of its ability to adapt to the special environment of volcanically devastated sites and the fact that its seed is easy to collect (Iwata et al. 2005). Thus, I first focused on its physiological advantages in an extremely volcanically devastated site (**Chapter 3**). In this chapter, I comprehensively studied the photosynthesis-related leaf traits of *M. condensatus* in response to different habitat conditions. This chapter was published by Zhang et al. (2020).
- 2) In order to fully understand the physiological and ecological characteristics of all pioneer species in Miyake-jima volcanically devastated site. I measured the leaf photosynthesis-related traits of *M. condensatus*, *A. sieboldiana* and *F. japonica* var. *hachidoensis* to determine their growth advantages in physiological and ecological characteristics (**Chapter 4**).

In the final chapter, I provide a general discussion regarding the physiological strategies of pioneer species in volcanically devastated sites.

2. Overview of the Study Area

2.1. Introduction to Miyake-jima Island

The Island of Miyake (Miyake-jima; 55.5 km² in area; 775 m at the highest point), an active basalt volcano, is located in the western rim of the Pacific Ocean (34°05'N, 139°11'E), approximately 180 km south of Tokyo and belongs to the Fuji volcanic southern zone in the East Japan volcanic belt (**Figure 2.1**). Miyake-jima is characterized by a humid, warm-temperate climate. Meteorological data (Meteorological Station at 36.2 m a.s.l. on the island) from 2000 to 2019, reported by the MetBroker Weather Station 476770, were as follows: a mean total annual precipitation of 2,827 mm (ranging from 2,042 mm (2013) to 3,951 mm (2003)) and minimum and maximum monthly precipitation of 138.3 mm and 328.2 mm, respectively. The annual mean, minimum, and maximum monthly temperatures were 18.5°C, 9.5°C and 26.1°C, respectively. The isolated island is exposed to strong winds (annual wind speed, 5.1 m s⁻¹) with frequent wind directions toward the southwest, west-southwest, and northeast. The recent geological eruptions of Miyake-jima occurred in 1940, 1962, 1983, and 2000, with about 20-year intervals (Tsukui et al. 2001). The main stratovolcano was formed by Pleistocene volcanic activity (Isshiki 1960; Miyazaki 1984). Within the recorded history, Miyake-jima Island had erupted 15 times by 1999. The recent eruptions before 2000 (1874, 1940, 1962 and 1983) were characterized by the ejection of basaltic scoria and outflows of aa lava.

The natural vegetation of Miyake-jima is a textbook example of primary succession represented by chronosequences of volcanic substrata of different ages. A climax stage of the vegetation type is an evergreen broad-leaved forest composed of *Castanopsis sieboldii*, *Machilus thunbergii* and *Camellia japonica*. The vegetation on

Miyake-jima Island has been disturbed by anthropogenic activities such as cultivation, clear-cutting for charcoal, and planting of *Cryptomeria japonica* for timber production. Most sites with moderate inclination on the old volcanic ejecta at lower altitudes are intensively cultivated, in parallel to the practice of a traditional agroforestry technique using *A. sieboldiana*, an N-fixing tree. Deciduous broad-leaved forests and shrubs composed of *A. sieboldiana*, *Prunus speciosa*, *Styrax japonica* var. *kotoensis* and *Weigela coraeensis* var. *fragrans* are distributed on younger substrata and on shifting cultivation fields.

The process of primary succession inferred from Kamijo et al. (2002) and from previous studies (Kamijo and Okutomi 1995) on Miyake-jima Island is summarized as follows: (1) successful colonization of deciduous *A. sieboldiana*, an N-fixing tree, on bare lava flows; (2) facilitation by N-fixation of *A. sieboldiana* and the colonization of seral deciduous species such as *P. speciosa* and climax evergreen spp. such as *M. thunbergia*; (3) rapid above-ground biomass accumulation and formation of a mixed forest; (4) disappearance of *A. sieboldiana* and *P. speciosa* under low-light conditions; and (5) replacement of dominant evergreen tree species from *M. thunbergii* to *C. sieboldii*.

2.2. The eruption of Miyake-jima Island in 2000

From July to September 2000, Miyake-jima erupted and ejected large amounts of volcanic ash, forming a large collapsed crater (> 1 km in diameter and > 400 m in depth). All the people were evacuated from the island in September 2000. Windborne material has covered extensive areas creating a new substrate. After the crater formation, large quantities of volcanic gas containing SO₂ and H₂S caused widespread defoliation, and the damage decreased at sites farther from the crater (Kamijo and Hashiba 2003),

particularly on the leeward side of Mt. Oyama (Kamijo and Hashiba 2003; Kato et al. 2005). Sulfur dioxide (SO₂) emissions peaked at 12,300 tons per day at the beginning of the eruption and then declined rapidly. Since 2010, the daily SO₂ emissions have reduced significantly and have gradually stabilized, nearing zero by August 2016 (Japan Meteorological Agency 2019). At the time of this study, there were no current effects of volcanic gas, as the emissions had already ceased. About 60% of the vegetation on the island was initially damaged by the heavy deposition of volcanic ash (Yamanishi et al. 2002). The map of the degree of vegetation damaged by the eruption in 2000 is shown in **Figure 2.2**. Different letters indicate different damage degrees. However, in contrast to the previous eruptions, the volcanic activity of 2000-2002 was characterized by the formation of a large crater together with the ejection of large amounts of volcanic ash and gas. This type of eruption had not been recorded for 2,500 years prior to 2000 (Tsukui et al. 2001).

2.3. Vegetation Recovery process in Miyake-jima volcanic succession

Previous studies by Kamijo et al. (2002, 2008) reported that there were three dominant pioneer species first invading and successfully being established in the early stage of the Miyake-jima volcanically devastated site (**Table 2.1**).

M. condensatus (**Figure 2.3**), a C₄ plant belonging to Poaceae, is one of the most typical pioneer species of volcanically devastated sites and can form dense growth, distributed across coastal areas of Japan, China, Korea, and the Pacific Islands. It is also tolerant to various environmental stresses (e.g., high salinity) (Hung et al. 2009). In Miyake-jima Island, *M. condensatus* is also an important pioneer species and appears to have high tolerance to SO₂ gas and acidic soils (Kamijo et al. 2008). *Miscanthus condensatus* notably increased notably following the eruption in 2000, and after more

than a decade of change, it is still the dominant species in most places; however, in some places its biomass and coverage have decreased due to light resource limitations from competitive species (Kamijo et al. 2008).

A. sieboldiana (**Figure 2.3**) is a deciduous N-fixing pioneer tree species. In Miyake-jima volcanically devastated sites, its faster above-ground biomass development is due to the facilitation effects of N-fixation. The inorganic N soil concentration was extremely high in locations where *A. sieboldiana* was dominant. The deposition of N from *A. sieboldiana* via litterfall would decrease the soil C/N ratio, which in turn facilitates net soil N mineralization and consequently provides an ample supply of inorganic N to nearby plants. N limitation on vegetation development, which is prevalent during the early stage of succession on volcanic lava flows or similar substrates elsewhere, is thus alleviated (Kamijo et al. 2002).

F. japonica is native to Japan, Taiwan and Korea. It is now widely naturalized in Europe and North America and is regarded as one of the worst invasive alien species. *F. japonica* was widely found in manmade and natural habitats but was restricted to open, sunny sites. *F. japonica* var. *hachidoensis* (**Figure 2.3**) is a perennial species of the family Polygonaceae. In Miyake-jima, the *F. japonica* is characterized by having thick leaves. As it has developed root systems, it could accumulate the necessary nutrients to ensure survival in the early stages of volcanic succession (Adachi et al. 1996).

2.4. Study sites

Based on the division of the damage degree of different areas on Miyake-jima Island (**Figures 2.2, 2.3**), combined with the present vegetation and habitat environment, three sites with significantly different light and soil characteristics were selected on

Miyake-jima Island. These three sites were designated as bare land (BL), shrub land with gap (SLG) and shrub land under canopy (SLUC), respectively.

In the current study, BL (**Figure 2.4A**) is one of the most disturbed areas created by the 2000 eruption of Miyake-jima Island. Vegetation establishment on this site was affected by the nearly complete loss of organic matter, the nature of the deposit, local climate conditions, high SO₂ concentration, surviving plant life in adjacent areas, and patterns of plant colonization and growth. In the BL, all original vegetation was completely buried by thick volcanic ash deposition after the eruption of 2000. Through more than 15 years of natural vegetation recovery, vegetation coverage has been significantly improved. However, since it was the closest to the eruption crater and suffered the maximum damage among the three sites, substantial bare land dominated the landscape. The successional process in the BL can be classified as primary succession because of the complete destruction of vegetation at the start of succession. Vegetation is very sparse and is composed of the pioneer species: *A. sieboldiana*, *M. condensatus*, and *F. japonica* var. *hachidoensis*. The land surface is still covered with unweathered volcanic ash, combined with low soil moisture content. Plants are completely exposed to sunlight. The height and density of the *M. condensatus* growing here are relatively lower than those of the other two sites.

At the site SLG (**Figure 2.4B**), a part of the original vegetation was buried by the relatively thick volcanic ash deposition after the eruption of 2000. However, the initial degree of damage was lower than that at BL. Over the last 15 years, pioneer species such as *M. condensatus* have dominated. *M. condensatus* at this site takes the absolute advantage. The N-fixing pioneer species *A. sieboldiana* is also distributed here. The light conditions of this site are better than those of SLUC and the soil nitrogen was better than that of BL.

At the site SLUC (**Figure 2.4C**), the degree of damage was the smallest among the three sites; therefore, some trees had survived through the eruption. The main types of vegetation cover are *A. sieboldiana* and *Eurya japonica* (the middle-successional stage species). The ground surface is covered with an abundance of litters and does not contain large amounts of volcanic ash. Combined with the effect of soil animals (e.g., earthworms) on the soil (Imoto unpublished data), the soil conditions at this site were the best among the three study sites. The presence of a relatively high wood has created poor understory light conditions in this area. At this site, the *M. condensatus* individuals are sparsely distributed, with some dead specimens discovered.

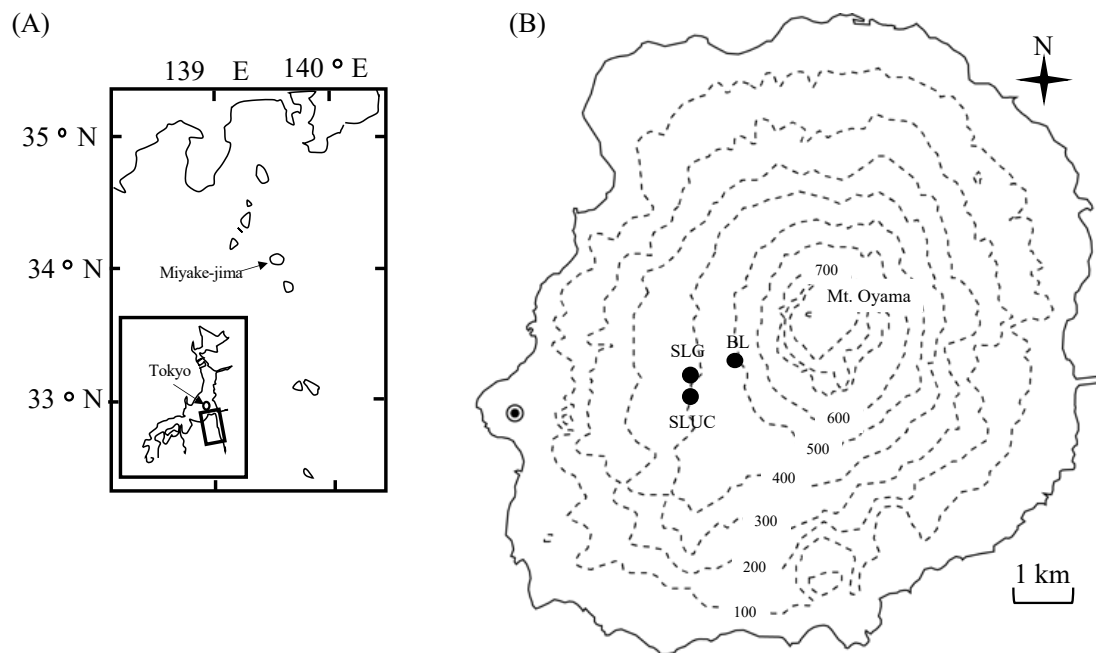


Figure 2. 1 Maps showing the location of the Island of Miyake (Miyake-jima) in the western rim of the Pacific Ocean (A) and the sampling sites and in this research (B).

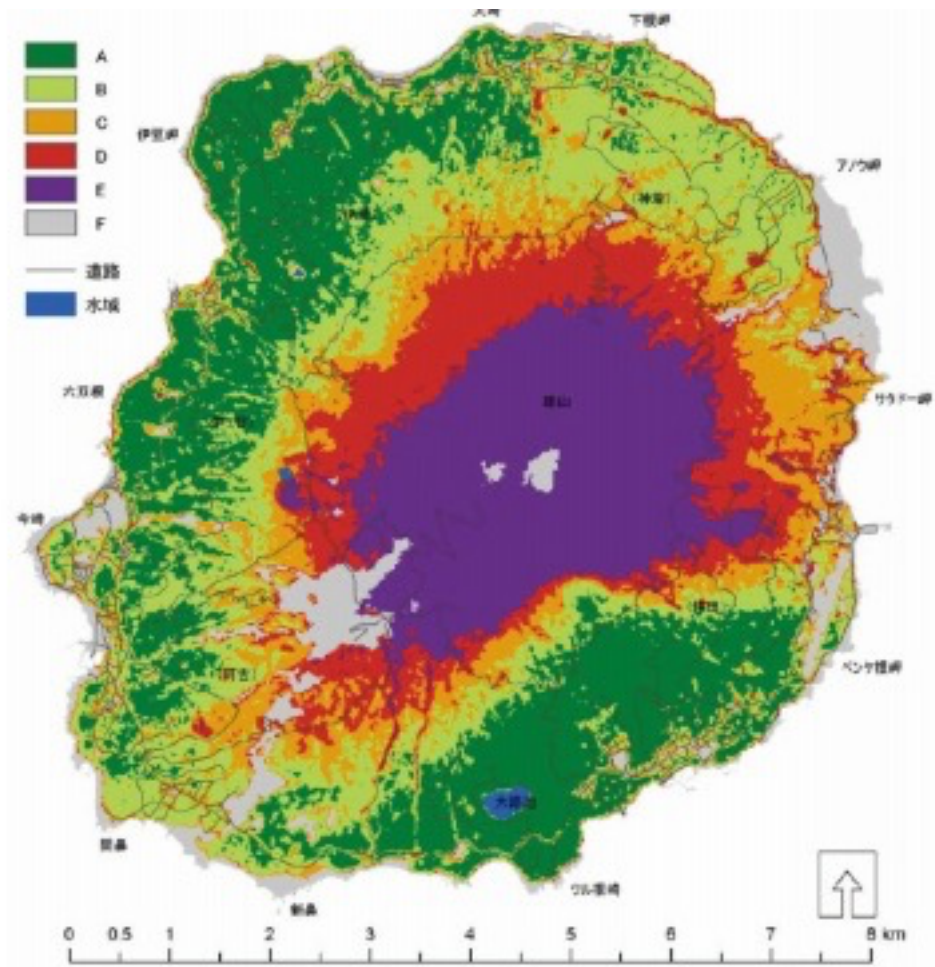
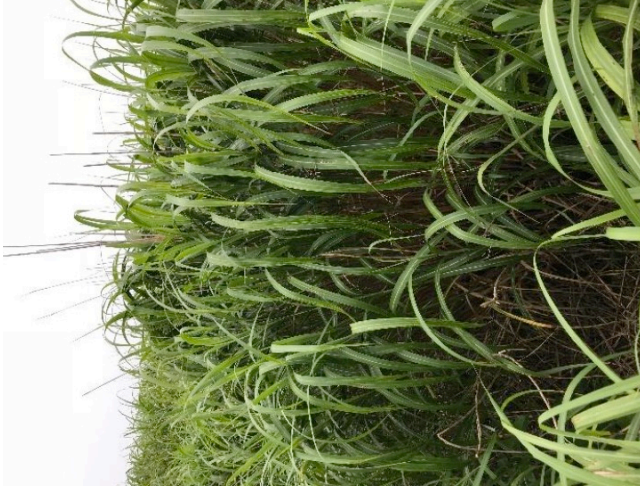


Figure 2. 2 A map of vegetation damaged by the 2000 eruption (Takahashi et al.2008).
 The letter means F: new crater, E: bare land, D: all trees buried or felled, C: defoliation of all trees, B: mixture of defoliated and normal trees, A: normal vegetation.

Alnus sieboldiana



Miscanthus condensatus



Fallopia japonica var. *hachidyoensis*



Figure 2. 3 Pioneer species in Miyake-jima island.



Bare land



Shrub land gap



Shrub land under canopy

Figure 2. 4 Landscape of study sites in Miyake-jima Island

Table 2. 1 Growth form, photosynthesis pathway, and N fixation ability of pioneer species in Mikake-jima volcanically devastated site

Family/species	Growth form	Photosynthetic pathway	N fixation ability
Poaceae			
<i>Miscanthus condensatus</i>	perennial grass	C ₄	non-N-fixing
Polygonaceae			
<i>F. japonica</i> var. hachidoensis	perennial herb	C ₃	non-N-fixing
Betulaceae			
<i>Alnus sieboldiana</i>	perennial tree	C ₃	N-fixing

3. Photosynthetic Properties of *Miscanthus condensatus* at Volcanically Devastated Sites on Miyake-jima Island

3.1. Introduction

Volcanic ecosystems are usually characterized by high levels of stress and disturbance (del Moral and Grishin, 1999). In early volcanic successional systems, plant growth is severely limited by nitrogen (N) (Vitousek et al. 1989; 1993). Plants inhabiting volcanic ecosystems have to withstand the lack of N, which limits their growth and ability to invade and establish new sites. Furthermore, surviving in volcanic devastated sites requires coordinated physiological responses (Ishikawa et al., 2007; Raavel et al., 2012; Fischer et al., 2019). Pioneer species seem to be highly adaptable to adverse environments. Many dominant pioneer species can adapt to environmental changes by adjusting their growth strategies (Dalling and Hubbell, 2002; del Moral and Eckert, 2005). For example, altered root morphology, improved resource use efficiency, resorption efficiency (e.g., N, P), and N-fixing ability are all important adaptation strategies that allow plants to cope with poor nutrient habitats. Many studies have focused on N-fixing pioneer species at new volcanically devastated sites (Kamiyo et al., 2002; Walker et al., 2003; Titus, 2009; Choi et al., 2014), because N is scarce in new volcanic materials, such as lava, scoria, and volcanic ash (Vitousek et al., 1989). However, there are also many pioneer species without the N-fixing ability in volcanic succession. This raises the question of how non-N-fixing pioneer species adjust their strategies to adapt to nutrient-deplete habitats. However, little research has been carried out on the physiological ecology of non-N-fixing pioneer species inhabiting harsh environments such as volcanic sites (Nara, 2006; Voronkova et al., 2008; Stefansdottir et al., 2014).

N plays a vital role in plant functioning and is one of the most important limiting nutrients in terrestrial ecosystems (Vitousek et al., 1989; Vitousek and Howarth, 1991). Leaf traits provide insights into the N use strategy of plants. Leaf N content (N_{area}), leaf mass per area (LMA), and light-saturated photosynthetic rate (A_{max}) are the main leaf traits correlated with each other (Wright et al., 2004; Ordoñez et al., 2009). Numerous studies have found that N_{area} is associated with abiotic factors, such as light availability (Seemann et al., 1987; Sims et al., 1998), nutrient availability (Crew et al., 1995; Guilherme Pereira et al., 2019), temperature (Cordell et al., 1998; Reich and Oleksyn, 2004), fire regime (Raison, 1979), and volcanic gas (Choi et al., 2014). The relationship between N_{area} and these abiotic factors reflects the adaptive response of the plant to the local environmental conditions. Many studies have demonstrated that the A_{max} and N_{area} were lower in N-deficient soil than in soil not limited in N (Warren, 2004; Li et al., 2009; Chen et al., 2014). Efficient use of N can determine the competitive ability (Rundel, 1982) and dominance of a plant in a given environment (Aerts and van der Peijl, 1993). Thus, efficient use of N is essential for pioneer species without N-fixing ability to successfully establish and grow in N-deficient habitats. Photosynthetic N-use efficiency (PNUE: the rate of net photosynthesis accomplished per unit N in a leaf), are frequently used as important leaf traits for characterizing leaf photosynthetic economics (Hikosaka, 2004). However, the pattern of change in PNUE under N-limited conditions has been inconsistent; studies have shown that PNUE values have increased (Chen et al., 2014; Zhang et al., 2016), decreased (Cao et al., 2007; Mu et al., 2016) and showed no marked variation (Boussadia et al., 2010) along N addition gradients. In addition, PNUE is negatively correlated with LMA and increases with higher A_{max} and N_{area} levels (Takashima et al., 2004; Wright et al., 2005). However, relatively little is known about the relationships of these traits of non-N-fixing pioneer species at volcanically

devastated sites.

Miscanthus, a genus of the Poaceae and a C₄ plant, have a wide distribution and are found across both the cool and warm temperate regions of East Asia (Hung et al., 2009). In Japan, two closely related species, *Miscanthus sinensis* and *M. condensatus* (neither have the N-fixing ability), are common dominant pioneer species in the early stages of volcanic succession (Tagawa, 1964; Hirata et al., 2007; An et al., 2008; Kamijo et al., 2008). In Miyake-jima Island, Japan, the site of focus in this study, *M. condensatus* was the most dominant species in the ecological recovery process following the volcanic eruption of large amounts of ash and gas in the year 2000 (Kamijo et al., 2008). According to a chronosequence study on lava flow of different ages, the process of primary succession on Miyake-jima Island can be summarized as follows: (1) successful colonization of pioneer species, such as deciduous *Alnus sieboldiana* (a N-fixing tree), *M. condensatus* (a perennial grass), and *F. japonica* var. *hachidoensis* (a perennial herb), on bare lava flows; (2) colonization of several deciduous species such as *Prunus speciosa* and climax evergreen species such as *Machilus thunbergii* and *Castanopsis sieboldii*, and the disappearance of pioneer species; and (3) establishment of the climax forest, composed of evergreen *C. sieboldii* (Kamijo et al., 2002). The successional process following the eruptions in 2000 differs from that on lava flow, and *M. condensatus*, the species of interest in this study, extensively dominated the new bare land (Kamijo et al., 2008). However, to the best of our knowledge, physiological studies of other pioneer species on volcanically devastated sites are limited (Vitousek et al., 1993; Sakata et al., 2006; Cordell et al., 2001) and no research has been conducted to understand the growth strategies of these two *Miscanthus* species through physiological traits. In addition, there are no quantitative studies of the PNUE of pioneer species on volcanically devastated sites.

Therefore, we hypothesized that the photosynthetic-related leaf traits, especially the PNUE in *M. condensatus*, play a role in the survival of this species, particularly when it grows in volcanically N-deplete soil.

To test this hypothesis, we examined (1) whether the *M. condensatus* displays any difference in photosynthetic-related leaf traits among different habitat conditions, and (2) how environmental factors influenced the photosynthetic-related leaf traits of *M. condensatus* in extreme volcanically devastated sites.

3.2. Materials and Methods

This study was conducted between 2017 and 2018 on a volcanically devastated site (17 and 18 years after the eruption). At the time of this study, the landscape of the area was composed of bare land, *M. condensatus* grasslands, and *A. sieboldiana* shrubs.

3.2.1. Research Area

This study was conducted at the Miyake-jima active volcanic island, Japan (34°05' N, 139°55' E), which covers an area of 55.44 km² and has an altitude of 775.1 m a.s.l. (Mt. Oyama). The island has a humid, temperate climate, with an average annual temperature of 17.7 °C, with the average temperatures of the hottest and the coolest month being 26.2 °C (August) and 9.6 °C (February), respectively. The annual precipitation is 2953.6 mm, and the average precipitation for the months with the minimum and maximum rainfall are 140.3 mm (December) and 383.3 mm (October), respectively (Japan Meteorological Agency) (<https://www.jma.go.jp/jma/indexe.html>). At the time of this study, there were no current effects of volcanic gas as the emissions had already ceased.

3.2.2. Experimental Design and Measurements

To examine the effects of environment conditions on the leaf traits of *M. condensatus*, three study sites in different successional stages were selected: bare land (BL) with *M. condensatus* patches (**Figure 2.4A**), a site with a relatively open tree canopy (SLG: shrub land gap), and a site with a closed canopy (SLUC: shrub land under canopy) (**Figure 2.4B, C**). In BL and SLG *M. condensatus* were the absolutely dominant species. The other species such as *A. sieboldiana* (N-fixing species) and *F. japonica* var. *hachidyoensis* (a perennial herb) were also existed sparsely. In SLG, the upper leaves of *M. condensatus* were almost fully exposed to ambient sunlight, while in SLUC, *M. condensatus* was sparsely distributed under the closed canopies, and some dead *M. condensatus* were found. The recovery of vegetation in the study area proceeded in a direction from lower to higher elevation, and from further away from the Oyama crater to closer to the crater (Takahashi et al. 2011). This recovery process may be caused by many factors, such as heavy wind and seed dispersal, the initial damage of volcanic ash and toxic gas (Takahashi *et al.* 2011). Thus, the three study sites fully reflected the recovery of the vegetation. In addition, differences in actual air temperature and wind caused by changes in altitude may also have affected plant growth in the study site.

In each study site, eight *M. condensatus* plants were selected for the measurement of leaf traits. The *M. condensatus* selected in BL were between 0.5 and 1.5 m in height. The distance between the selected plants was at least 5 m. In SLG and SLUC, the plants were between 1.8 and 2.3 m in height. In total, 144 leaf samples were measured. In each study site, leaf traits were measured at an interval of 1 month from July to October 2017 and from May to June 2018 (6 months in total) which contained the entire growing season of *M. condensatus*. The specific measurement time for each study site is shown in **Figure 3.4**. We measured a total of 48 leaves (eight leaves every month) at each study

site. All study sites were measured within 3 days of each other.

3.2.3. Gas Exchange Parameters

To measure the activities of healthy leaves located in the upper part of each sample, the second or third (counted from the top of the shoot) fully expanded leaves were selected every month. Based on continuous field observations (every month from May to October 2018), it was discovered that the leaves of *M. condensatus* in Miyake-jima Islands had a relatively short leaf life span (4 months), and that the production of new leaves was continuous throughout the growing seasons. The relative position of leaves became sequentially lower with the progression of seasons; therefore, leaf samples were collected from the same position in the plant for measurement to make sure they have similar leaf age. In addition, the sampled leaves were evaluated for the determination of LMA and leaf N every month. Intelligent portable photosynthesis system LCPro + (ADC BioScientific, UK) was used to calculate the measurement of gas exchange. At each study site, eight leaves (one leaf per plant) were measured per month. Measurements were taken from the leaves in the middle, and all gas exchange parameters were measured between 9:00 am and 11:00 am. During all of the measurements, the chamber CO₂ concentration, temperature, and vapor pressure deficit (VPD) were maintained at 420 μmol · mol⁻¹, 25 °C, and 1.0 kPa, respectively. Light-response curves were determined at irradiances between 2000 and 0 μmol · m⁻² · s⁻¹ using a built-in LED light source in seven photosynthetic photon flux density (PPFD) steps and were fitted using a non-rectangular hyperbola model (Thornley, 1976). A_{max}, and LCP were calculated using light-response curves. WUE was calculated as the ratio of A_{max} to the E at photosynthetic photon flux density (PPFD) saturation (Field et al., 1983).

3.2.4. Structural and Biochemical Characteristics of Leaves

When the measurements of photosynthetic parameters were completed, the sampled leaves were collected and wiped; the measured areas were cut out and scanned, and the images were processed using ImageJ software (National Institutes of Health, Bethesda, Maryland, USA, imagej.nih.gov/ij) for leaf area. For leaf dry mass/leaf area determination, cut-out leaf samples were dried at 80 °C for 48 h to constant weight and measured for their final weight. The remaining leaf samples were also dried for the determination of leaf N using an NC analyzer (SUMIGRAPH NC-220F). The PNUE was calculated as A_{\max} divided by N_{area} ($\text{PNUE}, \mu\text{mol} \cdot \text{CO}_2 \text{ mol} \cdot \text{N}^{-1} \cdot \text{s}^{-1} = A_{\max} (\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) / (1/14N_{\text{area}})$) (Poorter and Evans, 1998).

3.2.5. Chlorophyll Fluorescence

While measuring gas exchange parameters, three light-adapted leaves (the middle part) of each plant were selected for the measurement of chlorophyll fluorescence using MINI-PAM-II-Walz. The minimum fluorescence (F_0) and maximum fluorescence (F_m) were determined following a 30 min dark adaptation using leaf clips, in order to calculate the maximum photochemical efficiency of PSII (F_v/F_m).

3.2.6. Rainfall Distribution Before Measurements

To assess the effects of precipitation on the leaf traits of *M. condensatus*, the rainfall distribution before the measurement day of each month was analyzed. We used the 3-day integrated rainfall from before the photosynthetic measurements, from the daily rainfall data from the Japan Meteorological Agency (2019) (<https://www.jma.go.jp/jma/indexe.html>). The highest levels of rainfall (before the measurement day) were recorded in June and October (**Figure 3.3**).

3.2.7. Soil Measurements

In October 2017, soil samples from the root zones of the sampled *M. condensatus* plants were collected using 100 mL core samplers of 5 cm depth for the determination of the soil properties of the study sites. Surface soils (5 cm in depth) were collected because *M. condensatus* develops its root system on the ground surface and its fine roots are concentrated in shallow soils. Three cores were sampled from the soil around the root crown (approximately 10 cm away from the root crown) and were subsequently combined and mixed. After air-drying, the samples were passed through 2 mm and 0.5 mm sieves, respectively, and the roots were removed. Soil samples between 0.5 mm and 2 mm were ground to sizes lesser than 0.5 mm. The soil total C (STC) and STN were analyzed with SUMIGRAPH NC-220F, using samples smaller than 0.5 mm.

3.2.8. Light Measurements

Every time we measure photosynthetic parameters, Hemispherical photographs were taken using a Nikon Coolpix 990 and a Nikon FC-E8 Fisheye Converter (Nikon, Tokyo, Japan). Photographs were taken above each plant (totally, 48 were taken in each study site) and were analyzed to calculate canopy openness using Gap Light Analyzer (GLA Version 2.0) (Frazer et al. 1999). Canopy openness was defined as the fraction of open sky in the hemisphere that was visible from a point beneath the canopy and was used as an index of the light available to the *M. condensatus* plants.

A representative location was selected in the three sites for the measurement of photosynthetic photon flux density (PPFD) at sunny or cloudy days, with the aid of IKS-27 sunshine sensors (KOITO MANUFACTURING CO., LTD, Yokohama, Japan) which were mounted on poles at a height of 1 m. The measurements were done simultaneously in the three sites between 8:00 am and 4:00 pm in the month of August

2016 and reading of data was done every 30 s. We used maximum daily PPFD for each site and light-response curve for each leaf sample (48 samples in each study site) to estimate the actual photosynthetic rates (A_{actual}). This parameter can be used to explain the photosynthetic rate in natural light condition.

3.2.9. Data Analysis

All analyses were carried out using the statistical package R version 3.6.0 (R Development Core Team, 2018). For each leaf traits variable, data were analyzed by two-way ANOVA, with study sites and month as main fixed factors plus a site \times month interaction term (**Table 3.2**). The site differences of annual mean value of each leaf traits were compared (**Table 3.3**). Prior to analyses, the assumptions of normality and homogeneity of variances were tested using Shapiro–Wilk and Bartlett tests. For leaf traits that meets homogeneity of variance and normal distribution (E , N_{area} , LMA, A_{max} , PNUE), one-way ANOVA was applied to assess the differences of them followed by Tukey’s post hoc test used for multiple comparisons between the sites. A non-parametric Kruskal–Wallis test was performed to check for differences in environmental factors and some leaf traits (F_v/F_m , LCP, and WUE) among the three study sites. Steel Dwass post hoc test was performed to detect significant differences in the mean value of environmental factors, F_v/F_m , LCP, and WUE. The generalized linear mixed model (GLMM) with the package lme4 (Bates et al., 2015) was used to assess the effect of environment factors on leaf traits. The predictors (fixed effects) including the soil N, canopy openness, temperature and precipitation (3-day integrated rainfall), while the response variables were leaf traits (F_v/F_m , E , N_{area} , LCP LMA, and A_{max} , WUE, PNUE), respectively. The study site and month were included as random effect factors. Marginal and conditional R^2 were calculated.

3.3. Results

3.3.1. Study Site Description

Among three sites, in bare land (BL) and shrub land gap (SLG), *M. condensatus* were the absolutely dominant species. The other species such as *A. sieboldiana* (N-fixing species) and *F. japonica* var. *hachidyoensis* (a perennial herb) were also existed sparsely. In shrub land under canopy (SLUC), *M. condensatus* was sparsely distributed under the closed canopies, and some dead *M. condensatus* were found. Soil N (STN) (0–5 cm) and canopy openness varied significantly across the three study sites. In BL, STN was significantly lower than in SLG and SLUC. (**Table 3.1, $p < 0.05$**). However, there was no significant difference in STN between SLG and SLUC (**Table 3.1, $p > 0.05$**). Canopy openness value was relatively similar between BL and SLG (higher than 60%), while canopy openness in BL was significantly higher than that in SLUC (**Table 3.1, $p < 0.05$**). The maximum daily photosynthetic photon flux density (PPFD) among the three study sites reached $1227 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (BL), $531 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (SLG) and $102 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (SLUC) at noon, respectively (**Table 4.1**).

3.3.2. Monthly and Site Changes in Leaf Traits of *M. condensatus*

The main effect of site was statistically significant for most of the leaf traits of *M. condensatus* (**Table 3.2, $p < 0.05$**), whereas water use efficiency (WUE) and PNUE were not affected by site. In BL, *M. condensatus* had significantly lower N_{area} , A_{max} , maximum quantum yield of PS II (Fv/Fm), and transpiration rate (E), but significantly higher LMA and WUE than those in the SLG or SLUC (**Table 3.3, $p < 0.05$**). Light compensation point (LCP) value in the SLUC was significantly lower than that in the

BL and SLG (**Table 3.3, $p < 0.05$**), but the difference in mean between BL and SLG was not significant. In terms of PNUE, there was no significant difference in values from the three sites (**Table 3.3, $p > 0.05$**).

During the growing season, F_v/F_m , E , N_{area} , LMA and WUE, showed significant monthly changes (**Table 3.2, $p < 0.05$**), and relative values among the three sites varied in each month (Figure 1). The site by month interaction was significant for all leaf traits of *M. condensatus* (**Table 3.2, $p < 0.05$**). In the BL, the A_{max} , E , and PNUE values in October 2017 and June 2018 were higher than those recorded in the other months (**Figure 3.1b, d, h**); also, the PNUE values in these two months were higher in the three sites (**Figure 3.1h**). **Figure 3.2** shows the estimated actual photosynthetic rates (A_{actual}) in the three sites. The A_{actual} in SLUC only reached 23–30% of the A_{actual} recorded in SLG.

3.3.3. Effect of Environment Factors on the Leaf Traits of *M. condensatus*

Based on the generalized linear mixed model (GLMM) results (**Table 3.4**), canopy openness had significant positive effects on the F_v/F_m , LMA and LCP. No association between canopy openness and the remaining leaf traits was found. STN had a significant positive effect on N_{area} and A_{max} . The precipitation had significant positive effect on A_{max} and PNUE. As for PNUE, both canopy openness and STN significantly affected it negatively (**Table 3.4**).

3.4. Discussion

3.4.1. Advantages of *M. condensatus* in Leaf Traits at Miyake Volcanically Devastated Site

Our aim in this study was firstly to examine photosynthetic-related advantages of

M. condensatus in volcanically devastated sites. Normally, N_{area} for C_4 plants is considered to range from 1.68 to 2.52 $\text{g} \cdot \text{m}^{-2}$, while that of C_3 plants ranges from 2.80 to 3.64 $\text{g} \cdot \text{m}^{-2}$ (Ehleringer and Monson 1993). Ghannoum et al. (2005) reported a N_{area} range of 0.48 to 1.23 $\text{g} \cdot \text{m}^{-2}$ for C_4 NADP-ME grasses. An analysis by Kattge et al. (2011) reported an average of $0.93 \pm 1.45 \text{ g} \cdot \text{m}^{-2}$ for 232 C_4 grass species. Compared to the above research reports, the present study reported N_{area} values within the normal range for *M. condensatus* despite the low soil N content. In addition, it should be noted that the soil N in the BL was about 10% of that in SLG; however, the N_{area} reached 70% of what was recorded in SLG (**Table 3.3**). This seems to indicate that *M. condensatus* has a unique nitrogen acquisition conservation strategy in extreme N-limited habitats.

Values of A_{max} for *M. condensatus* ($18.81 \pm 3.72 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) in BL were lower than in SLG and SLUC (**Table 3.3**). However, it should be noted that *M. condensatus* achieved 75% A_{max} compared to that in SLG despite low soil N conditions. Generally, C_4 grasses have a high capacity for photosynthesis. Kattge et al. reported (2011) an A_{max} value of $19.78 \pm 1.58 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ based on 97 species of C_4 grass in various conditions. However, the A_{max} of *M. condensatus* ($18.81 \pm 3.72 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) in BL was not drastically lower than this value. All these above indicated that the photosynthetic advantages of *M. condensatus* in Miyake.

To further evaluate the photosynthetic adaptive advantage of *M. condensatus* in the volcanically devastated site, its photosynthetic activity was compared to those of plants growing in other nutrient-poor habitats (e.g., sand dunes, glacier retreated sites, volcanic deserts). A recent study in Australia's sand dunes compared the photosynthetic activity of several species across three different successional stages, including the early stage of primary succession (Guilherme Pereira et al., 2019). Seven pioneer species (not including C_4 grass species) growing in the early stage of primary succession (plant

growth is limited by N) had A_{\max} values ranging from 11.3 to 17.8 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Guilherme Pereira et al., 2019). The highest A_{\max} value was reported for the native shrub species, *Acacia rostellifera*. Compared to the species monitored by Guilherme Pereira et al. (2019), *M. condensatus* appears to have a higher photosynthetic capacity in the early stage of primary succession. However, there are no comparable studies which investigated photosynthesis of C_4 plants in volcanic deserts. In terms of C_3 plants, including trees, there are a few studies comparable to our data. Choi et al. (2014) reported that the A_{\max} value for *A. sieboldiana* (an N-fixing C_3 tree species) at Miyakejima Island, in a site with low exposure to the disturbances from the 2000 eruption, was 12 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. This value is lower than that recorded for *M. condensatus*, even though the study site was highly disturbed and had low soil N. In the volcanically devastated site of Mt. Fuji, Japan, Sakata et al. (2006) reported the photosynthetic rate of two C_3 herb species, *Reynoutria japonica* and *Aconogonum weyrichii*. Both species inhabited an old volcanic desert (last eruption at 1707) exposed to heavy wind, and they had A_{\max} values of 18.60 and 22.70 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for *R. japonica* and *A. weyrichii*, respectively. On the other hand, the A_{\max} value of *M. condensatus* appears to be higher than that of *Metrosideros polymorpha*, a C_3 tree species in Hawaii (Cordell et al., 2001). The A_{\max} values of *M. polymorpha* species growing on a 26-year-old lava flow (from an eruption in 1959) and on a 195-year-old lava flow (from an eruption in 1790) in the Kilauea Iki crater were 8.68 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 8.54 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively (Vitousek et al., 1993; Cordell et al., 2001). These comparisons support the finding that *M. condensatus* has a higher photosynthetic capacity in nutrient-poor habitats.

PNUE describes leaf photosynthetic economics, and plants with higher PNUE values are regarded as being more adaptive to N-deplete habitats. In general, C_4 plants have higher PNUE than C_3 plants (Brown, 1978; Schmitt and Edwards, 1981; Sage and

Pearcy, 1987). Kattge et al. (2011) reported the average PNUE value of 80 C₄ grasses as $263.34 \pm 23.23 \mu\text{mol} \cdot \text{CO}_2 \text{ mol} \cdot \text{N}^{-1} \cdot \text{s}^{-1}$, which is similar to the value recorded for *M. condensatus* in the present study. We also found that there was no significant difference in PNUE among three study sites. This indicated that the advantages in N use strategy of *M. condensatus*. However, there are no reported studies on the PNUE of species growing on similar nutrient deplete habitats; hence, there is no basis for comparison with the PNUE of *M. condensatus*. This higher PNUE of *M. condensatus* appears to be primarily a result of its C₄ pathway (Ghannoum et al. 2005), which can eliminate photorespiration by increasing CO₂ levels in the vicinity of the enzyme Rubisco. However, to fully understand the relative adaptability to N poor habitat among C₄ grass, further comparative studies are necessary.

3.4.2. Physiological Cause for the Variation in PNUE

The GLMM results showed that there were significant negative effects of STN on PNUE, positive effect on N_{area} and A_{max}, and no effect on LMA (**Table 3.4**). This is consistent with the conclusions of several preceding studies that a higher PNUE facilitates the establishment of plants (Sage and Pearcy, 1987; Ghannoum et al., 2005; Uribe-larrea et al., 2009). However, in the present study, the effect of the different sites on PNUE values was not significant (**Tables 3.2 and 3.3**). This is because PNUE is the ratio of A_{max} to N_{area} and the common trend observed in them as a result of soil N levels may be responsible for the non-significant difference in PNUE values between the three study sites. As for the physiological causes of PNUE variation, numerous studies focused on inter-species differences in PNUE suggest that an increase in PNUE with increasing LMA is caused by decreasing photosynthetic rates and lower N partitioning into Rubisco compared to higher N partitioning into cell walls (Poorter and Evans,

1998; Onoda et al., 2004; Takashima et al., 2004). However, in this study (about a single species), it was discovered that LMA did not significantly reduce PNUE (**Table 3.3**). This is consistent with a previous study, which reported similar PNUE but different LMA values, 40–50 g · m⁻² and 15–20 g · m⁻² in the leaves of *Chenopodium album* grown in low nutrient and high average light intensity, and those grown in high nutrient and low average light intensity, respectively. In addition, it was observed that the main factor affecting LMA in the present study was the light condition (**Table 3.4**). Hikosaka (2004) also suggested that within a single species, differences in PNUE do not occur when LMA changes with growth light or nutrient availability. Therefore, in evaluating the physiological factors responsible for the variation in PNUE in *M. condensatus*, it is necessary to investigate the relationship between PNUE and the allocation of N among the major foliar N fractions. In addition, GLMM shows the strong positive relationship between precipitation and PNUE. During the growing season, A_{max}, PNUE showed strong monthly changes, and relative values among the three habitats in each month also varied (**Figure 3.1, Table 3.2**). In BL, A_{max} increased in June and October (**Figure 3.1d**), and the PNUE value in these two months was also markedly higher among the three habitats (**Figure 3.1c**). All the changes observed in June and October occurred when measurements were carried out after rainfall. The rainfall in June and October were higher than in other months (**Figure A 3.1**). These are consistent with the previous finding that temporal rainfall may help plant growth (Xiong et al. 2017; Hu et al. 2019) and indicate that *M. condensatus* in BL are more sensitive to water deficits. Water deficit is another factor that limits growth, and probably had a large effect on *M. condensatus* grown in newborn soil. In this study, under water stress, *M. condensatus* could not perform all its photosynthetic abilities. Therefore, in the Miyake-jima volcanically devastated site, the photosynthetic capacity of *M. condensatus* is achieved

when there is a sufficient water supply. The site-specific pattern of *M. condensatus* responses to rainfall suggests that rain may be an important contributor to the growth and survival of *M. condensatus* on the volcanically devastated site.

3.4.3. Physiological Responses to Light Availability

Light availability gradients affect leaf traits, which determine leaf carbon acquisition (Baldocchi and Harley, 1995; Sands, 1995), and previous studies have demonstrated that leaves that inhabit low-light environments exhibit shade-acclimatized traits in the long run (Sims and Pearcy, 1991; Lewis et al., 2000). Results from this study indicated that under low light environments (SLUC), *M. condensatus* had significantly lower LMA and LCP (**Table 3.2**), but higher Fv/Fm than those exposed to higher light intensities. The GLMM shows a strong positive relationship between canopy openness and Fv/Fm. These results demonstrate that *M. condensatus* acclimatized to the shade by decreasing LCP and by increasing its ability to capture light (higher Fv/Fm). The higher Fv/Fm observed in SLUC (**Table 3.2, Figure 3.1**) suggests that *M. condensatus* leaves are more efficient at trapping light in the pigment range of PSII under low light conditions (Maxwell and Johnson, 2000), enabling them to use light during the constant low-light periods in the SLUC. In addition, Fv/Fm can provide insights on the ability of plants to tolerate environmental stresses and the extent to which those stresses can damage their photosynthetic apparatus (Maxwell and Johnson, 2000). Results from this study indicated that extremely low soil N did not significantly affect Fv/Fm (**Table 3.3**). This also proves the high resistance of the species to environmental stress. Furthermore, reduction in LMA is a typical shade acclimatization response, which can improve the light harvested per unit of resource invested in the construction of photosynthetic tissue (Sims et al., 1998; Grassi and

Bagnaresi, 2001).

Although the capacity to photosynthesize and grow under shaded conditions has been proven in this study, due to the limitation of the actual light condition, the actual photosynthesis rate in SLUC was not high (**Figure 3.4, Figure 3.9**). The low A_{actual} in SLUC indicates that the productivity of *M. condensatus* is low under low-light conditions. The lower productivity of *M. condensatus* under the pioneer trees of *A. sieboldiana* can explain the successional change from grassland consisting of *M. condensatus* to shrub land comprising *A. sieboldiana* and other tree species (Kamijo et al., 2008).

3.5. Conclusions

We investigated the leaf traits of *M. condensatus*, a non-N-fixing pioneer species that grows in Miyake-jima, a volcanically devastated site. The results showed that compared to previous studies and internal comparison of Miyake Island, *M. condensatus* could maintain a relatively higher N_{area} , A_{max} despite under extreme N-deficient conditions. This is partly as a result of its higher PNUE. PNUE in *M. condensatus* appears to be high even for a C_4 grass; this is a characteristic necessary for its successful growth in N-deficient soils. The higher PNUE of *M. condensatus* may be an intrinsic function of its C_4 pathway. We also found that PNUE values in BL were higher than in the other two habitats in June and October. Considering the level of rainfall before our measurements, the higher PNUE in BL was related to rainfall.

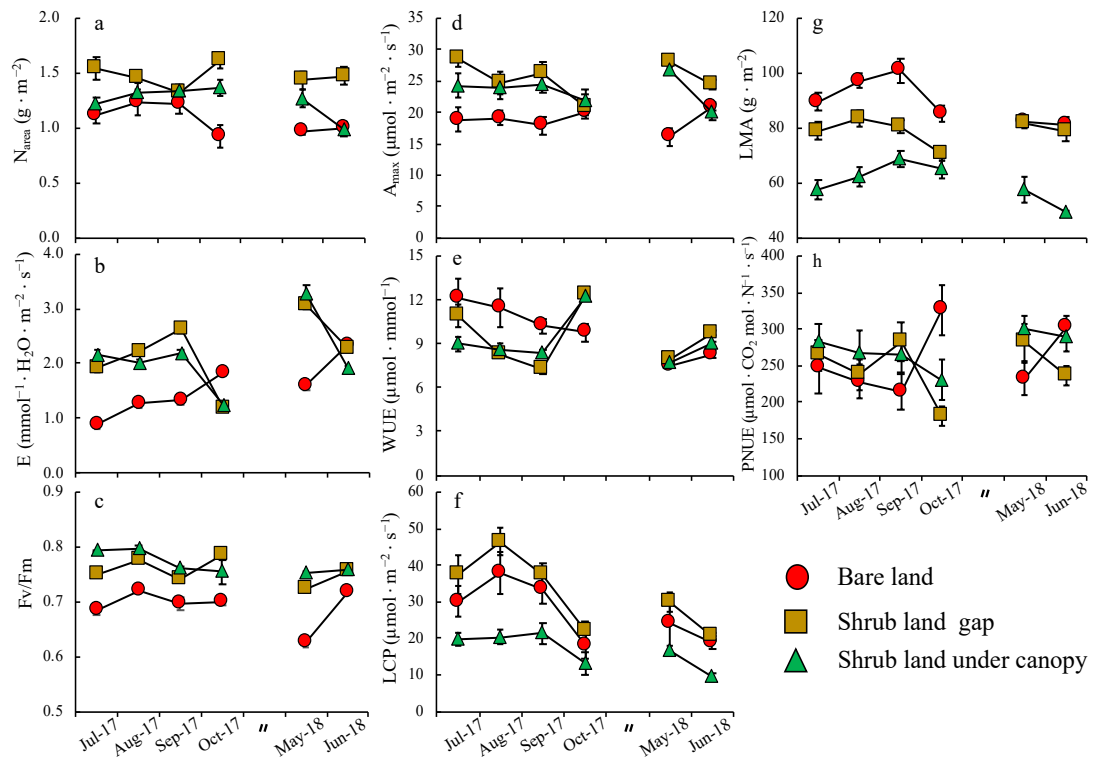


Figure 3. 1 Monthly changes of leaf traits.

Leaf N content (N_{area}) (a); transpiration rate (E) (b); maximum quantum yield of PSII (Fv/Fm) (c); light-saturated photosynthetic rate (A_{max}) (d); water use efficiency (WUE) (e); light compensation point (LCP) (f); leaf mass per area (LMA) (g); photosynthetic N use efficiency (PNUE) (h) in bare land (BL) (circle), in shrub land gap (SLG) (square) and in shrub land under canopy (SLUC) (triangle). Vertical bars represent the mean \pm SE (n = 8).

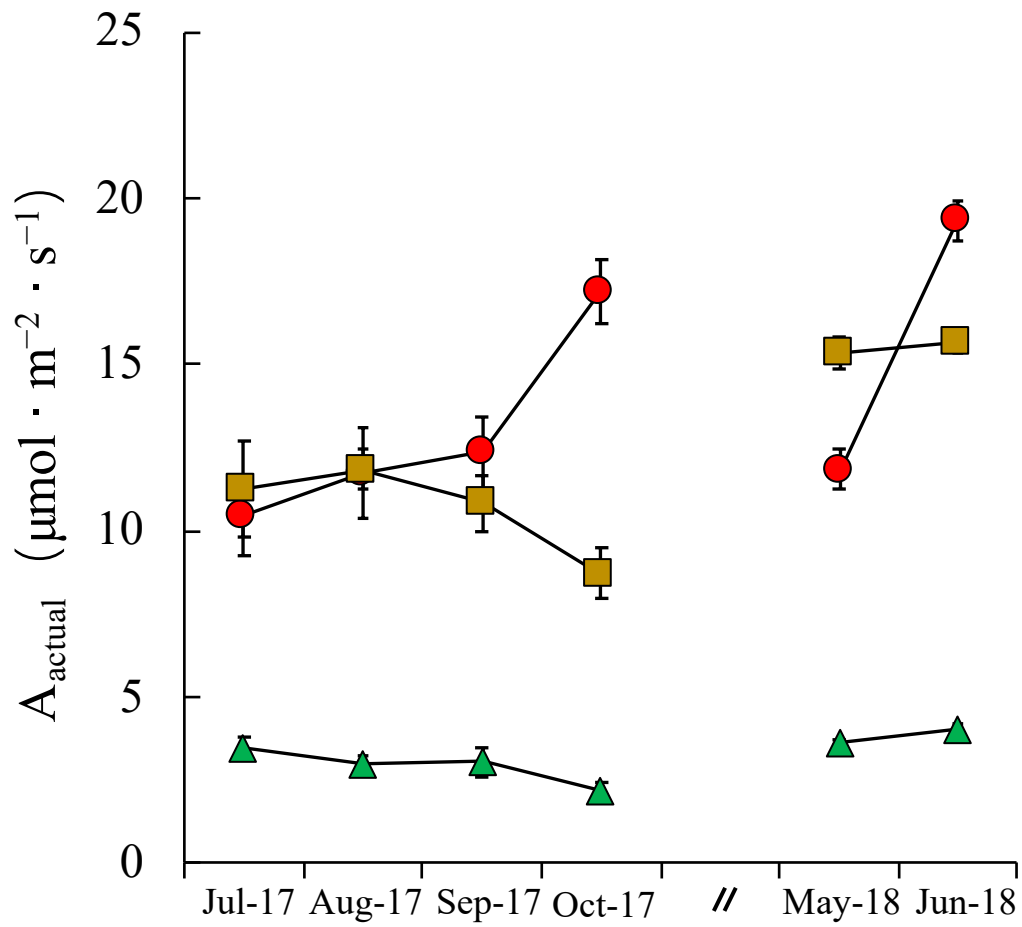


Figure 3. 2 Monthly changes of estimate actual photosynthetic rates (A_{actual}) under actual ambient maximum photosynthetic photon flux density.

M. condensatus grown in BL (circle), in SLG (square) and in SLUC (triangle). Vertical bars represent the mean \pm SE (n = 8).

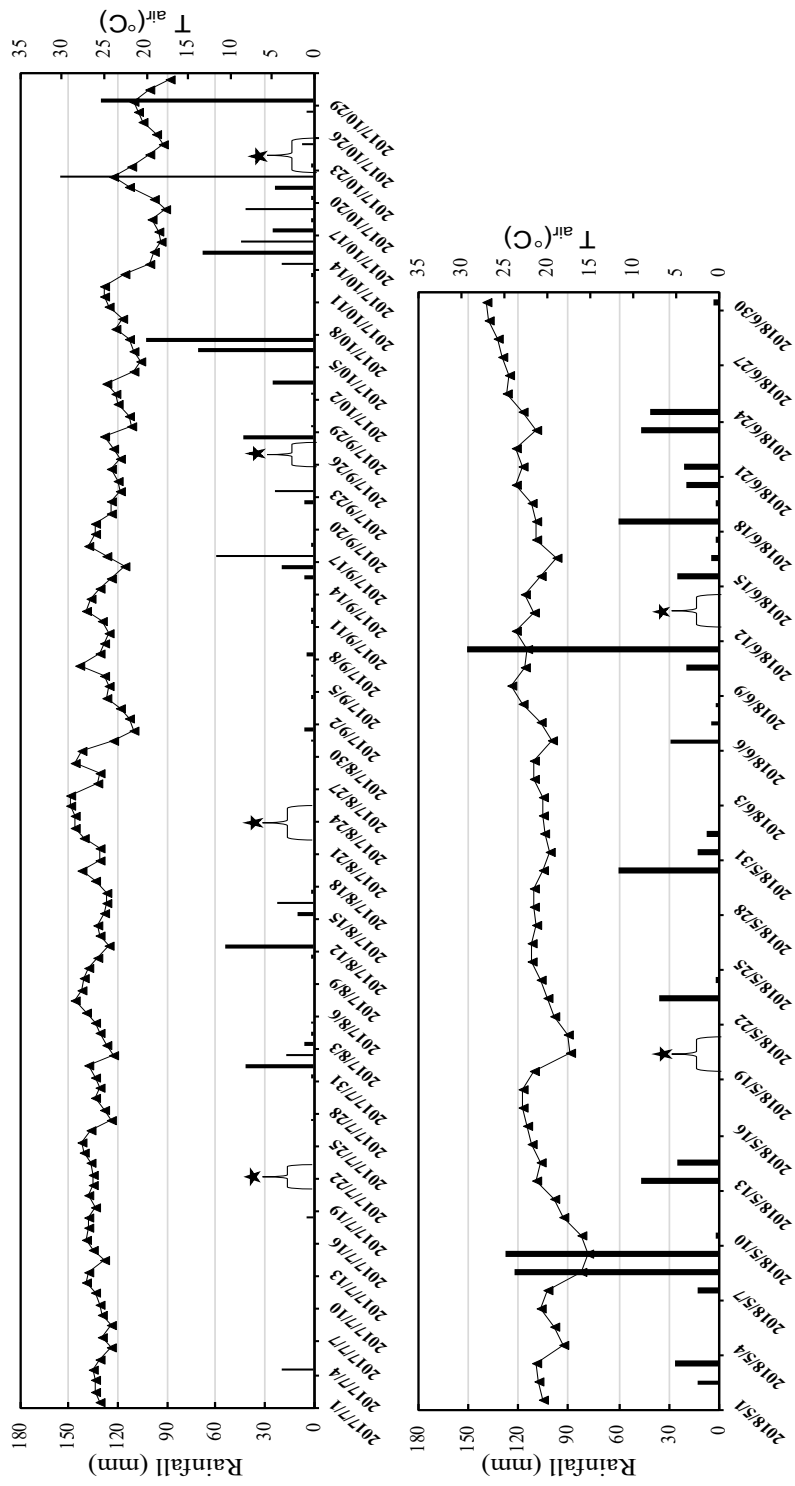


Figure 3. 3 Daily rainfall (bars) and daily average air temperature (T air) (solid line) from June 2017 to July 2018. Pentagonal star represents the survey implementation day. Data is from Japan Meteorological Agency (2019).

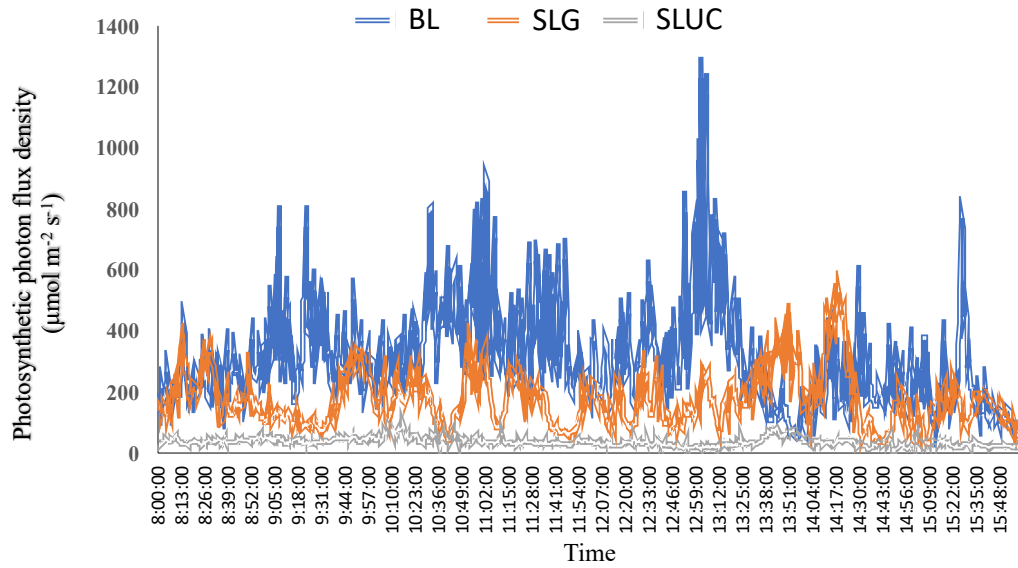


Figure 3. 4 Patterns of photosynthetic photon flux density in three study site 16th August 2016

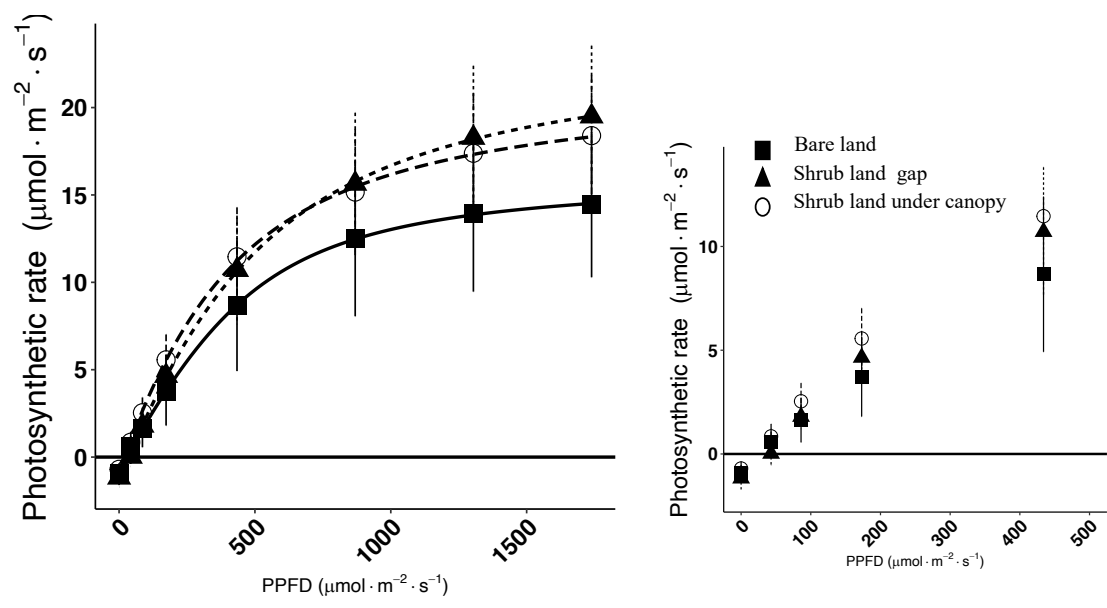


Figure 3. 5 Photosynthetic light response curves of current year leaves of *M. condensatus* grown at the Bare land, Shrub land gap, and Shrub land understory. Values are the means (\pm SD).

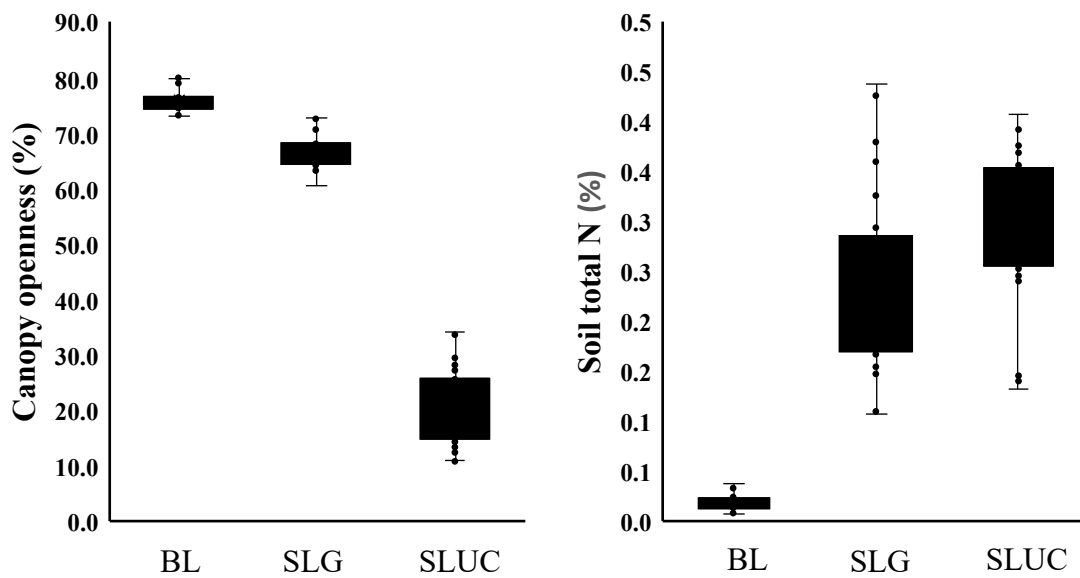


Figure 3. 6 Canopy openness and soil total N among three sites.

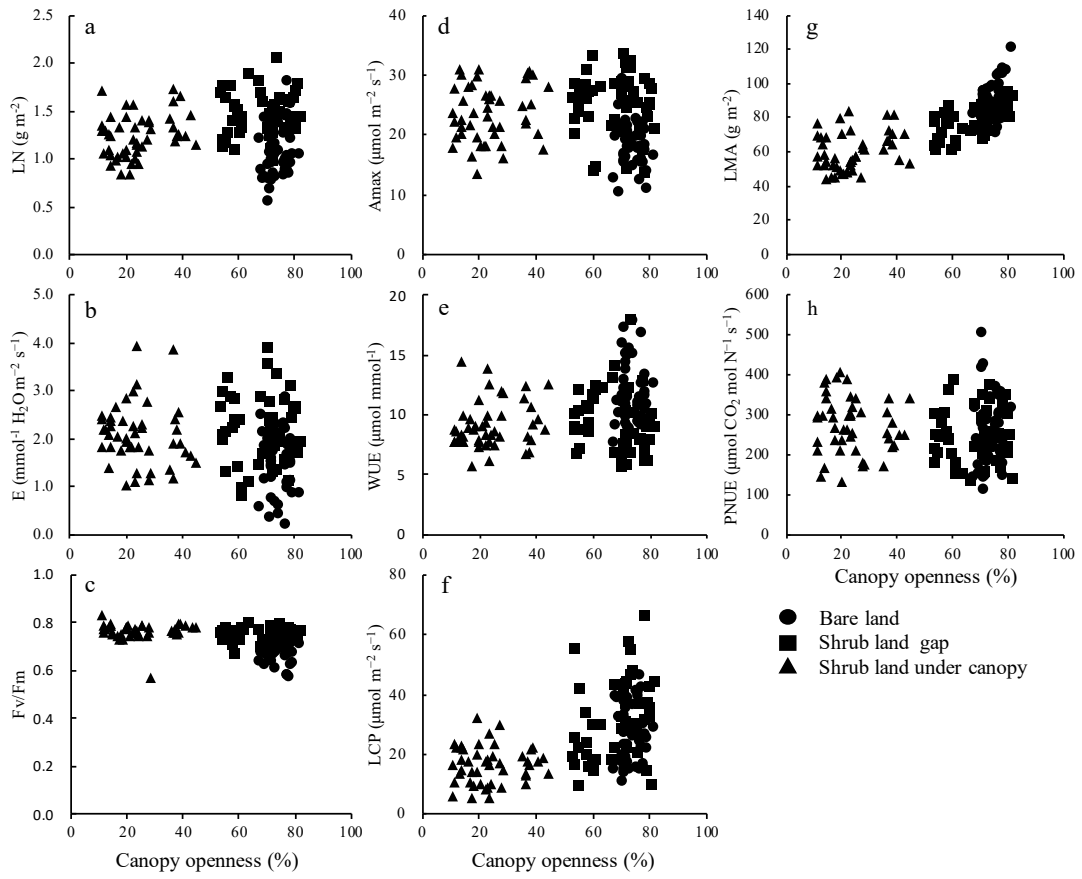


Figure 3.7 Relationships of leaf traits and canopy openness.

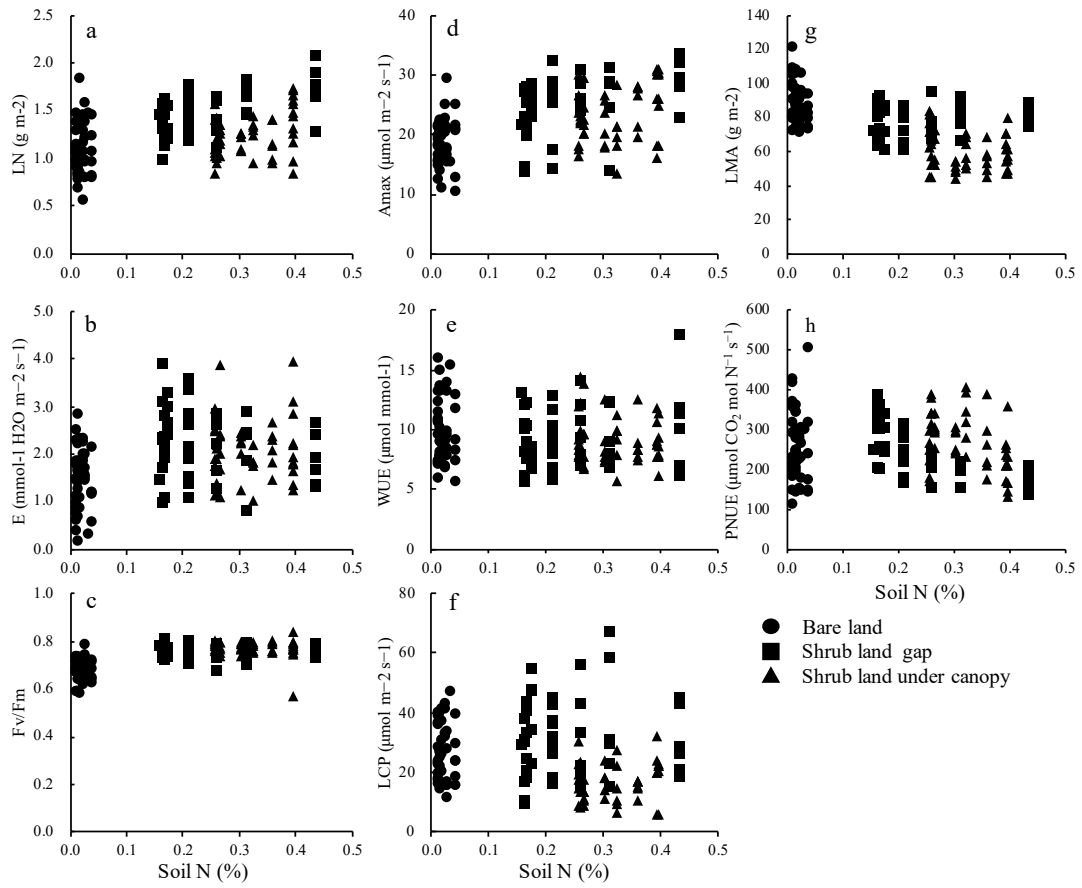


Figure 3. 8 Relationship of leaf traits and soil N.

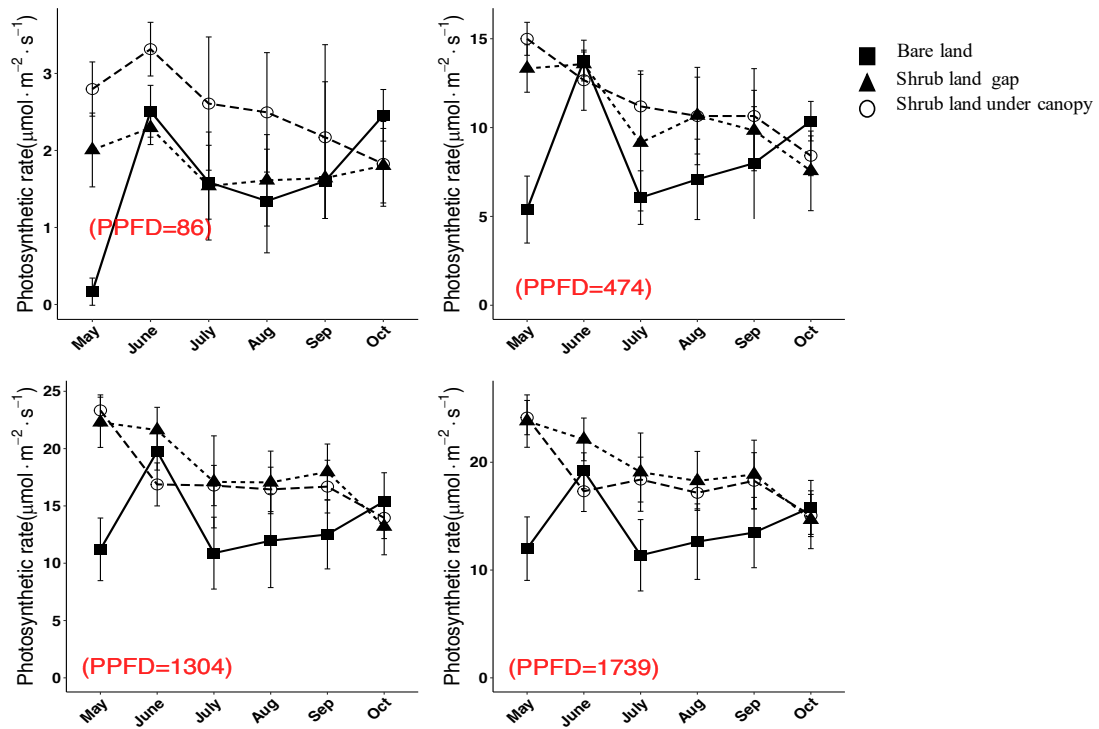


Figure 3. 9 Photosynthetic rate under different PPFD value among three sites

Table 3. 1 Location and morphometric characteristics of bare land (BL), shrub land gap (SLG) and shrub land under canopy (SLUC).

Factor	BL	SLG	SLUC
Location	34°04.689'N, 139°30.816' E	34°04.790'N, 139°30.245' E	34°04.790'N, 139°30.245' E
Altitude (m a.s.l)	500	400	400
Ash depth (cm)	30–35	30–35	30–35
Air temperature (°C)	25.54	26.16	25.64
Maximum PPFD ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	1227	531	102
Canopy openness (%)	74 \pm 0.5 a	68 \pm 1.3 a	24 \pm 1.4 b
STN (%)	0.02 \pm 0.002 b	0.24 \pm 0.02 a	0.30 \pm 0.01 a
STC (%)	0.20 \pm 0.03 b	4.54 \pm 0.68 a	5.78 \pm 0.42 a

Different letters indicate significant differences between the study sites revealed by Steel Dwass post hoc test at a significance level $p < 0.05$ after Kruskal–Wallis test. Abbreviations are meters above sea level (m a.s.l); photosynthetic photon flux density (PPFD); soil total N (STN) (n = 30); soil total carbon (STC) (n = 30); Canopy openness (n = 48).

Table 3. 2 The F values of two way-ANOVA for effects of site, month and their interactions on each leaf traits (n = 144) of *M. condensatus*.

Leaf Traits	Site	Month	Site:Month
Fv/Fm	133.359 ***	18.826 ***	5.682 ***
E (mmol ⁻¹ · H ₂ O m ⁻² · s ⁻¹)	44.21 ***	31.2 ***	14.32 ***
N _{area} (g · m ⁻²)	40.372 ***	2.31 *	2.796 **
LCP (μmol · m ⁻² · s ⁻¹)	39.24 ***	8.59 ***	2.95 **
LMA (g · m ⁻²)	140.834***	8.301***	2.901 **
A _{max} (μmol · m ⁻² · s ⁻¹)	32.03 ***	1.666	2.837 **
WUE (μmol · mmol ⁻¹)	2.76	3.82 **	2.779 **
PNUE (μmol · CO ₂ mol · N ⁻¹ · s ⁻¹)	1.624	0.927	3.067 **

Abbreviations are maximum quantum yield of PSII (Fv/Fm); transpiration rate (E); leaf N content (N_{area}); light compensation point (LCP); leaf mass per area (LMA); light-saturated photosynthetic rate (A_{max}); water use efficiency (WUE); photosynthetic N use efficiency (PNUE). Significance of the coefficients: * p < 0.05, ** p < 0.01, *** p < 0.001.

Table 3. 3 Leaf traits of *M. condensatus* (Mean value \pm SE; n = 48) in bare land (BL), shrub land gap (SLG) and shrub land under canopy (SLUC).

Leaf Traits	BL	SLG	SLUC
Fv/Fm	0.69 \pm 0.05c	0.75 \pm 0.03b	0.77 \pm 0.05a
E (mmol $^{-1}$ · H ₂ O · m $^{-2}$ · s $^{-1}$)	1.51 \pm 0.05b	2.22 \pm 0.06a	2.05 \pm 0.07a
N _{area} (g · m $^{-2}$)	1.07 \pm 0.25c	1.47 \pm 0.22a	1.24 \pm 0.22b
LCP (μ mol · m $^{-2}$ · s $^{-1}$)	27.08 \pm 3.53a	32.54 \pm 1.89a	16.74 \pm 1.02b
LMA (g · m $^{-2}$)	89.29 \pm 11.11a	79.04 \pm 8.61b	60.03 \pm 10.98c
A _{max} (μ mol · m $^{-2}$ · s $^{-1}$)	18.81 \pm 3.72c	25.44 \pm 4.91a	23.56 \pm 4.65b
WUE (μ mol · mmol $^{-1}$)	12.29 \pm 1.17a	9.39 \pm 0.21b	9.73 \pm 0.20b
PNUE (μ mol · CO ₂ mol · N $^{-1}$ · s $^{-1}$)	258.79 \pm 82.75a	247.49 \pm 65.66a	272.56 \pm 69.82a

Abbreviations are maximum quantum yield of PSII (Fv/Fm); transpiration rate (E); leaf N content (N_{area}); light compensation point (LCP); leaf mass per area (LMA); light-saturated photosynthetic rate (A_{max}); water use efficiency (WUE); photosynthetic N use efficiency (PNUE). For E, N_{area}, LMA, A_{max}, and PNUE, different letters indicate significant differences between the study sites revealed by Tukey's post hoc test at a significance level $p < 0.05$ after one-way ANOVA. For Fv/Fm, LCP and WUE, different letters indicate significant differences between the study sites revealed by Steel Dwass post hoc test at a significance level $p < 0.05$ after Kruskal–Wallis test.

Table 3. 4 Effect of environment factors on each leaf traits (n = 144) of *M. condensatus*

(generalized linear mixed model—GLMM).

Traits		Estimate	Std. Error	<i>p</i>	MR ²	CR ²
Fv/Fm	Canopy openness	-0.0009	0.0004	*	0.22	0.63
	STN	0.0091	0.0398	ns		
	Precipitation	-0.00003	0.0001	ns		
	Temperature	0.0015	0.0013	ns		
E (mmol ⁻¹ H ₂ O · m ⁻² · s ⁻¹)	Canopy openness	-0.0106	0.0057	ns	0.18	0.70
	STN	-0.3054	0.6187	ns		
	Precipitation	0.0074	0.0013	***		
	Temperature	0.0123	0.0218	ns		
N _{area} (g · m ⁻²)	Canopy openness	0.0028	0.0019	ns	0.35	0.63
	STN	1.5840	0.2406	***		
	Precipitation	-0.0004	0.0004	ns		
	Temperature	-0.0103	0.0081	ns		
LCP (μmol · m ⁻² · s ⁻¹)	Canopy openness	0.8896	0.1060	***	0.50	0.95
	STN	-3.4123	10.0378	ns		
	Precipitation	-0.0098	0.0183	ns		
	Temperature	0.5708	0.2922	ns		
LMA (g · m ⁻²)	Canopy openness	0.6461	0.0793	***	0.75	0.85
	STN	-15.6300	10.1579	ns		
	Precipitation	-0.0223	0.0192	ns		
	Temperature	0.6693	0.3565	ns		
A _{max} (μmol · m ⁻² · s ⁻¹)	Canopy openness	0.0181	0.0376	ns	0.539	0.802
	STN	40.6600	4.7130	***		
	Precipitation	0.0247	0.0087	**		
	Temperature	0.2123	0.1616	ns		
WUE (μmol mmol ⁻¹)	Canopy openness	0.0064	0.0098	ns	0.04	0.42
	STN	0.2923	1.7096	ns		
	Precipitation	-0.0080	0.0050	ns		
	Temperature	0.1058	0.0810	ns		
PNUE (μmol · CO ₂ mol · N ⁻¹ · s ⁻¹)	Canopy openness	-1.9851	0.4008	**	0.34	0.45
	STN	-404.9090	60.8571	***		
	Precipitation	0.4855	0.1341	***		
	Temperature	3.0690	2.3935	ns		

Response variables are maximum quantum yield of PSII (Fv/Fm); transpiration rate (E);

leaf N content (N_{area}); light compensation point (LCP); leaf mass per area (LMA);
light-saturated photosynthetic rate (A_{max}); water use efficiency (WUE); photosynthetic
N use efficiency (PNUE), respectively. MR^2 Significance of the coefficients: ns $p >$
0.05, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3. 5 The specific measurement date in bare land (BL), shrub land gap (SLG) and shrub land under canopy (SLUC).

Measurement date	Study site		
	BL	SLG	SLUC
21-Jul-17	○		
22-Jul-17		○	
23-Jul-17			○
23-Aug-17		○	
24-Aug-17	○		
25-Aug-17			○
26-Sep-17		○	
27-Sep-17			○
28-Sep-17	○		
23-Oct-17		○	
25-Oct-17			○
26-Oct-17	○		
19-May-18	○		
20-May-18		○	
21-May-18			○
13-Jun-18	○		
14-Jun-18		○	
15-Jun-18			○

4. Comparison of the Photosynthetic Properties across Three Pioneer Species on Volcanically Devastated Sites in Miyake-jima Island

4.1. Abstract

In chapter 3, I comprehensively explained the leaf physiological characteristics of *M. condensatus*. In Miyake-jima volcanically devastated site, there also exist other pioneer species which inherently differing in photosynthetic pathway and N fixing ability. They commonly affect the local environment. In this chapter, I fully investigate the leaf photosynthesis-related traits of the three pioneer species (*M. condensatus*, *Fallopia japonica*, *Alnus sieboldiana*) in Miyake-jima volcanically devastated site.

Materials and Methods

This study was conducted at the Miyake-jima active volcanic island, Japan (34° 05' N, 139°55' E). The research site in this chapter focuses on the most severely devastated site (BL), I measured the leaf physiological traits of three pioneer species (*M. condensatus*, *Fallopia japonica*, *Alnus sieboldiana*) co-occurring in single natural volcanic habitat to determine their survival strategies, respectively.

Leaf physiological traits (i.e., morphological, physiological) of three pioneer species including leaf N content (Narea), light-saturated photosynthetic rate (Amax), and photosynthetic N use efficiency (PNUE), in three contrasting study sites: bare land (BL), shrub land gap (SLG), and shrub land under canopy (SLUC) were determined. The environment factors including the soil total nitrogen, canopy openness, temperature and precipitation (3-day integrated rainfall) were measured to assess the effect of environment factors on leaf physiological traits.

Results and Discussion

My results indicated that the three pioneer species living in the volcanically

devastated site of Miyake-jima island show significant differences in growth strategies. Although the Narea of N-fixing species *A. sieboldiana* was significantly higher than that of the species without N-fixing ability. However, the Amax of *A. sieboldiana* was not significantly high among three species. This is mainly due to PNUE of N-fixing species (*A. sieboldiana*) was lower than non-N-fixing species (*M. condensatus*, *F. japonica*). About the traits difference of two non-N fixing species, *M. condensatus* shows more strategy of resources acquisitive, whereas *F. japonica* shows more conservative strategies. The respective growth strategies of the three species make them successfully live in Miyake-jima volcanically devastated site. *A. sieboldiana* gather and fixes the nitrogen element in the soil through its root nodules, and stores the N in the leaves (e.g., high Narea), although PNUE is low, it can also maintain relatively high photosynthetic rate. *F. japonica*, although there is no N-fixing ability, it can maintain relatively high level of Narea, as it has high N resorption efficiency. *M. condensatus*, Also, there is no N-fixing ability, due to high PNUE, it can maintain high photosynthetic rate despite low Narea.

These fundamental knowledges could give us a deeper understanding of the mechanism of early-stage volcano primary succession and play a certain role in the restoration of volcanic ecology.

5. General Discussion

Since nearly all species in all communities participate in successional interactions, and physiological ecology encompasses everything that a plant does during its life cycle, a complete review of the physiological ecology of all species in all successional stages is necessary. However, even for the physiological ecology of pioneer species, fundamental ecological knowledge (e.g., leaf photosynthesis-related traits) is still relatively lacking. On Miyake-jima volcano Island, the pioneer species *A. sieboldiana*, *F. japonica*, and *M. condensatus* played a vital role in the recovery of the entire ecosystem of the devastated site. This study discusses the physiological importance of three pioneer species from 1) the differences in leaf traits and 2) the meaning of ecological development and succession (**Chapter 4**).

5.1. Comparison among the three pioneer species

My results indicated that all three pioneer species have the ability to adapt to the Miyake-jima N-deficient environment. They invaded and established in Miyake-jima volcanically devastated sites almost simultaneously. However, given that N input from precipitation is too low, *A. sieboldiana* is more advantageous for adapting to the Miyake-jima extreme N-deficient environment in terms of N-fixing.

Chapter 4 indicated that the three pioneer species showed a different suite of leaf traits that were closely related to their growth strategies (**Table 4.1**). These significant differences are mainly due to their inherent characteristics (e.g., whether they have the ability to fix nitrogen and their photosynthetic pathway (C₃ or C₄)). It is generally believed that N-fixing species have relatively high leaf N content (Matson 1990; Kamijo et al. 2002), and it has been thought that high N_{area} compensates for the restriction of photosynthesis under severe conditions in these areas (Körner and Diemer

1987; Cordell et al. 1999). In the present study, due to its N-fixing ability, the N_{area} of *A. sieboldiana* was the highest among the three pioneer species. Conversely, C_4 photosynthetic pathway species usually have higher photosynthetic capacity and N-use efficiency than C_3 species. This was also consistent with the results of my research, in which *M. condensatus* whether compared to other commonly occurring pioneer species (**Chapter 4**) or compared to its own growth in relatively high-nutrient habitats (**Chapter 3**); *M. condensatus* showed a high photosynthesis rate (A_{max}) and photosynthetic N-use efficiency (PNUE). In addition, despite the extremely low soil N content, *M. condensatus* can maintain relatively high leaf N content (N_{area}). According to **Chapter 4**, *F. japonica*, however, as a species that has neither has the N-fixing ability nor a special photosynthetic pathway, showed relatively high N_{area} (in comparison to that of *M. condensatus*) and A_{max} (in comparison to that of *M. condensatus*), and these two leaf traits of *F. japonica* were not significantly affected by soil N content. In addition, the soil N content under *F. japonica* and *A. sieboldiana* was not significantly different. Although these were similar to the results from *A. sieboldiana*, I believe that it plays a different role in volcanically devastated sites. *F. japonica* in BL showed a significant high LMA among the three species (**Chapter 4**). The LMA is part of an entire suite of interconnected traits that together shape the performance of plants. High-LMA leaves seem to be built to persist (Pérez-Harguindeguy et al. 2003). Owing to a better defense against herbivores and physical hazards, there is a positive correlation between LMA and leaf longevity in the field (Wright et al. 2004). In addition, species with an inherently high LMA not only have a greater leaf lifespan but also of roots system (Ryser 1996), thereby more efficiently conserving the acquired nutrients and carbon. A high leaf and root longevity enhance the residence time of nutrients in plants, thus providing high-LMA species with a competitive advantage on nutrient-poor soils

(Aerts and Chapin 1999). These differences in the suite of leaf physiological traits determine their respective advantages and ensure that they can successfully survive in the Miyake-jima volcanically devastated sites.

5.2. The importance of pioneer species on N microcirculation

As previously mentioned, in contrast to P, N is absent from most primary substrates. (Vitousek and Walker 1987). Accordingly, biologically available N should be in relatively short supply early in soil development - and organisms with the capacity to fix N₂ from the vast pool in the atmosphere should have a substantial advantage over those that cannot fix N. where N fixers are absent, N must be accumulated from fixed N in precipitation and some plant remains such as dead trees (Vitousek et al. 1993). In Miyake-jima volcanically devastated site, *M. condensatus* and *F. japonica* use N more efficiently than *A. sieboldiana*. In addition to their high resorption of N from senescing tissues (Matsuda unpublished data). As a consequence, both leaf and litter N concentrations are low. Moreover, the low-N litter of the two non-N fixing species immobilizer N longer during decomposition, causing N release to lag behind mass loss in *A. sieboldiana*. Overall, the effect of feedback is to slow rates of N cycling. However, high A_{max} value causing by PNUE conversely increasing the ecosystem productivity. For *A. sieboldiana*, the effect of feedback conversely fast rates of N cycling and hence increase N availability within Miyake-jima volcanically devastated site. Consequently, all these three species play an important role in development of the Miyake-jima volcanic ecosystem.

5.3. Impact of pioneer species on volcanic ecosystem development

Pioneer species such as C₄ grasses (e.g., *M. condensatus*) (Tagawa 1964; Hirata et al. 2007; An et al. 2008; Kamijo *et al.* 2008), nitrogen-fixers (e.g., lupine and alder)

Urtia japonica) (Masuzawa et al., 1991; Sakata et al. 2006) are generally considered to facilitate ecosystem development and succession through increases in soil fertility, amelioration of harsh environmental conditions, and perhaps reduced the water stress due to shading by their overstory. In Miyake-jima volcanically devastated sites, the rapid colonization of the three pioneer species (with different growth advantages) first ameliorated the local harsh environmental conditions overall. As for their respective contributions to the development of the ecosystem, *A. sieboldiana* (N-fixer) not only increased the soil N availability, but we also found that in the most extreme habitat on Miyake-jima Island (BL), the *A. sieboldiana* acts as a nurse plant, creating safe microsites, favoring the establishment and growth of understory species (including *M. condensatus*). In addition, leaf traits are good predictors of plant performance through their effects on ecological factors, in turn directly controlling particular ecosystem processes. For *M. condensatus*, a higher photosynthetic capacity and N/water-use ability which are related to plant size and growth rate, are particularly important for ecosystem development because they directly determine the productive capacity. For *F. japonica*, I believe that its higher light capture capacity causes its high contribution to energy exchange for ecosystem development. In summary, these three pioneer species promote the development of volcanic ecosystems by improving soil nitrogen availability and energy exchange.

5.4. Effects of interactions among plants on the succession mechanism in Miyake-jima volcanically devastated sites

All plants need the same resources of light, nutrients, water and space, yet these requirements differ among species and change during the life history of each species. Most plants modify their immediate environment in some way that can impact the

establishment and growth of both other species and other individuals of the same species. The responses of different species to these environmental changes can drive succession. Wright and Mueller-Dombois (1988) found that early pioneer species growing on volcanic cinders in Hawaii were adapted to higher light intensities and had deeper roots than those of the subsequent group of colonists; habitat improvement under shrubs improved establishment only in the latter group.

In the view of facilitation, in Miyake-jima volcanically devastated sites, all three species have a promoting effect on late-successional species such as *E. japonica* and *M. thunbergii*. Given its N-fixing ability, *A. sieboldiana* is considered to be the strongest pioneer, and a similar promoting effect of N fixers (*Alnus viridis* and *Lupinus lepidus*) on late-successional species was also suggested in the primary succession on Mount St. Helens (Titus 2009). In addition, there is also a competitive relationship among these three species. The adaptation of plants to different intensities of light helps explain species replacement in succession (Tilman 1986). Among these three pioneer species, due to high light requirements, I believe that some competition exists among the three species. *A. sieboldiana* has a competitive advantage in light interception because it is a tree that can reach a height of up to 15 m. In Chapter 3, we found that the photosynthesis rate of *M. condensatus* growing under *A. sieboldiana* was lower. As for *M. condensatus*, its high density and relatively large tussock make it hinder the establishment and growth of the other two species. Due to the competitive advantage of the above two species for light, *F. japonica* might not reach as high density as *M. condensatus*.

Consequently, the promoting effect among the three species is small; however, the *A. sieboldiana* may have a facilitating effect on the other two species by N fixation. Through their interactions (competition, facilitation, nutrient inputs, and defense stresses), the species composition and vegetation structure quickly change. I

hypothesize that in the early succession of Miyake-jima Island, the following physiologically driven mechanisms existed: 1) *A. sieboldiana* gathers and fixes the nitrogen element in the soil through its root nodules and stores the N in its leaves. Then, by means of litter, the volcanically devastated sites have comparable biological N input, creating relatively good soil conditions for other pioneer species without N-fixing ability. 2) Owing to the developed root system and high LMA of *F. japonica*, the residence time of N in *F. japonica* became long and further increased the residence time of N in the early stages of the volcanic ecosystem. 3) *M. condensatus* simultaneously quickly invaded and became the dominant species, relying on the relatively good environmental conditions (mainly soil N availability) and its own physiological advantages (high photosynthetic capacity, N-use efficiency, and water-use efficiency); this causes the early stage of the Miyake-jima volcanic ecosystem to be quickly developed.

5.5. Restoration using pioneer species

Our results additionally provided some suggestions for volcanic ecosystem restoration. These key leaf physiological traits that characterize photosynthetic capacity, resource-use capacity, and light-interception capacity can provide some useful suggestions for the artificial restoration of volcanic ecology in species selection. Although *M. condensatus* does not have N-fixing ability, its high photosynthetic capacity combines with better resource-use efficiency, making it a good candidate for restoration in Miyake-jima volcano ecosystem. Conversely, because N fixation is recognized as a trait that enhances the supply of the most frequently limiting nutrient, the introduction of nitrogen-fixing species is a management tool that is often used to enhance the productive potential of devastated sites (Bradshaw 1983). Thus, in the

Miyake-jima volcanically devastated sites, in combination with the N-fixation ability of *A. sieboldiana*, I believe that the restoration using these two pioneer species would be more successful.

5.6. Applications and future directions

This research focused on the physiological characteristics of pioneer species in recent Miyake-jima, where volcanic ash has been deposited for 17–18 years since the eruption in 2000. The three pioneer species in the Miyake-jima volcanically devastated sites exhibited their physiological advantages. This fundamental knowledge could provide a deeper understanding of the mechanism of early-stage volcano primary succession and play a certain role in the restoration of volcanic ecology. However, some questions still need to be clarified:

1. In the present study, we found that the C₄ grass *M. condensatus* showed a high value of PNUE, and this was one of the advantages allowing *M. condensatus* to successfully live in the volcanically devastated Miyake-jima sites. However, the physiological mechanism underlying high PNUE remains unclear. I think that to examine whether the high PNUE in N-poor soils is explained by the allocation of N among leaf N fractions is necessary.
2. In the present study, to avoid the effect of leaf age on the photosynthetic properties of *M. condensatus*, we selected the leaves with similar growth days. However, the seasonal changes in physiological traits are also necessary to allow us to better understand the overall physiological changes. Of course, this necessity also applies to *A. sieboldiana*, and *F. japonica*.
3. The present study mainly focused on the physiological traits of pioneer species communities, however, the physiological traits of middle- and late-successional

species remain unclear. In order to explain the succession mechanism from physiological insights, it is worth quantifying the physiological traits of middle- and late-successional species.

To answer the above-mentioned questions, much deeper and more extensive research is needed.

6. Acknowledgment

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7. References

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