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Bottom-up Regulation for Protection and Conservation of Forest Ecosystems in Northern Japan under Changing Environments

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Abstract

Many studies have emphasized the essential role of the bottom-up regulation induced mainly by herbivores of stable forest ecosystems. Most plants species are able to change the quality of their leaves after having been grazed by insect herbivores. This alteration may further enhance the natural defenses of the plant as well as the stability of the biodiversity of forest ecosystems. The effects of defoliation on the defense responses of deciduous broad-leaved trees was summarized from the viewpoint of plant-animal interactions. An outbreak of biological damage to newly introduced species was found on larch plantations in northern Japan. Introducing the hybrid larch F1 that developed by Hokkaido Forest Research Institute, prevented widespread damage to larch plantations. This is an example of bottom-up regulation of forest ecosystems. The defensive chemicals in leaves (condensed tannin and total phenolics) increase with a rise in foliar C/N. The defense chemicals in birch, willow and oak species were induced by grazing insect larvae, but not by mechanical cutting. Except for white birch, the amount of foliar defensive chemicals of three mid and late successional species (oak, elm and maple) was higher than, ash and alder. Under elevated CO₂ conditions, the chemical composition of plant foliage changed greatly, which may affect the activities of insect herbivores. The potential for improving forest management systems in changing environments using the forest's own defenses against herbivores, especially in relation to plant-insect interactions, is discussed for keeping forest vitality and health.

Key words: Bottom-up regulation, induced defense, hybrid larch, allocation of photosynthates, increasing CO₂

1. Introduction

The role of natural enemies in the stability of a forest ecosystem has been emphasized in the concept of "top-down" regulation (Koricheva *et al.* 1998, Ohgushi 1999). In general, nearly 10% of forest tree foliage is consumed as secondary production (Cry and Pace 1993, Ohgushi 2003) or "grazing" by insect herbivores. However, this rarely results in tree mortality. With progress in the study of interactions between plants and insect herbivores (Crawley 1997, Kamata 1999, Wada and Nagamoto 1999) and in the analysis of foliar chemicals (Schoonhoven *et al.* 1998, Koike *et al.* 2003a, Matsuki *et al.* 2003), the defensive capabilities of plants are seen as a "bottom-up" process (e.g. Price 1992, Walker and Jones 2001).

After grazing by insect larvae, most plants will change the quality and quantity of defensive chemicals in leaves but will rarely die (e.g. Haukioja and Honkenen 1997, Karban and Baldwin 2001, Lei 2002). Also, grazed plants sometimes provide "new nests", i.e. habitat for the subsequent insect larvae. A typical example is found in willow species growing along river basins. This has led to a new understanding of the web

of interaction between plants and herbivores in a forest ecosystem (Ohgushi 1999).

However, it takes a relatively long term to establish a "new web of interaction", and is usually measured in geological time. New plantations normally suffer from the threat of several biological stresses, even though sites are carefully selected to avoid physical stress, e.g. low temperature, flooding, etc. Moreover, atmospheric CO₂ is increasing at the speed of ca. 1.5ppm per year, which may create further interactions between plants and animals (Lincoln *et al.* 1993, Lindroth 1995, Koike *et al.* 2001, Bale *et al.* 2002). The behaviour of insect herbivores may also be strongly influenced by temperature as a result of global warming (Bale *et al.* 2002). Therefore, we need a deeper understanding of the interactions between plants and animals if we are to predict the damage that may be caused by biological stress. Based on this analysis, we hope to propose new methods of pest control in forest ecosystems, especially in secondary forests where species richness is usually high.

In this report, we will first give a brief history of creating larch plantations as an example of the

transplantation of a new species. Secondly, we will summarize several ideas for an understanding of plant-animal interactions in different environmental conditions. Finally, we will review changes in the chemical and physical composition of foliage traits under elevated CO₂ conditions to consider the possible interactions between plants and animals in future environmental conditions.

2. Transplantation of species

Northern Japanese larch (*Larix kaempferi*) plantations are examples of transplanting a new species to a new local ecosystem. Many conifer plantations across the country were planted because of the tree's uniform shape and high production rate (e.g. Asada and Satoo 1981). Other typical species used for afforestation were: Sugi cedar (*Cryptomeria japonica*) throughout Japan, Hinoki cypress (*Chamaecyparis obtusa*) in the southwestern part of the country, larch and Sakhalin fir (*Abies sachalinensis*) in northern Japan. In Hokkaido, the northern major island, huge areas of secondary and coppice forests were cut and reforested with Japanese larch. According to the plantation records, the shape of the plantation area is almost the same as the shape of Hokkaido Island (Koike et al. 2000). The aboveground production rate of larch is estimated to be similar to that of evergreen conifers (e.g. *Picea abies*) in cool-temperate environments (Matyssek 1985). However, the non-native Japanese larch in Hokkaido, which was transferred from central Japan, has a high susceptibility to disease and grazing damage by voles. Newly introduced species often suffer from several biological and physical problems. Similarly, birch (especially Monarch birch; *Betula maximowicziana* Regel) trees in Hokkaido also suffer from several different types of damage (e.g. Hara 2000). The following briefly summarizes the biological stresses affecting larch and birch plantations, and naturally regenerated birch (Photo. 1).

3. Biological stresses on larch and birch

3.1. Larch species

Voies, under snow cover, feed upon the larch stem at both the seedling and sapling stage (Hayashi et al. 1985, Kojima 1999, Orihashi et al. 2000). Trees with grazed cambium will die the following spring after the needle flush. This type of damage seriously inhibits the establishment of man-made forests in northern Japan. Mature larch is also damaged by insects (Bark beetle; *Ips cembrae*) and fungi (*Ceratocystis piceae*) after various stresses, such as the damage brought by typhoons (Yamaguchi et al. 1991). The bark beetle first attacks decaying trees and acts as a vector in spreading fungal infection. Large areas of forest have been destroyed by this beetle in Japan (Maeto et al. 1991). In contrast, the grazing damage on larch foliage by insect larvae, larch sawflies (most common species *Pristiphora erichsoni*) and the larch casebearer (*Coleophora longisignella*), rarely causes the death of individual trees.

A serious disease in larch, especially during the "young" stage is "shoot blight" caused by *Guignardia*

lacricina (Sawada) Yamamoto et K. Ito (Yokota 1966). Larch trees infected with shoot blight assume an umbrella shape because shoots at the terminal region (i.e. canopy top) are destroyed. However, adult trees rarely die from such damage while the disease generally kills seedlings. If we hope to stop the spread of diseases such as this, it is important to create wind shelters to protect against disease diffusion.

Originally, establishing secondary larch plantations in central Japan were hampered by root diseases (Ito 1966, Ota 2002). At first, diseased larch seedlings will wilt followed by death, which was believed to be induced by alleropathy or an imbalance of nutrients (Asada and Satoo 1981). Numerous examinations revealed, however, that the disease is caused by the fungi, *Armillaria mellea* (Vahl.) Qukl. and related species (e.g. Ota 2002).

Root or butt rots are found in areas of shallow water. If ambient humidity is high, the percentage of stem decay increases. The percentage of larch root/butt rot was greatest in young plantations of around 25 years of age, while that of stem rot progressively increases with stand age of up to 50 years for larch forests located in the southern part of Hokkaido Island (e.g. Igarashi and Takeuchi 1985).

3.2. Birch species

Monarch birch (*Betula maximowicziana*) plantations are also susceptible to attack by voles and hares (Hayashi et al. 1985, Rousi et al. 1996). Hares graze on birch shoots during winter, but the diffuse porous wood of the birch allows water transport from root to leaves even though stem was grazed. However, by the end of early summer, the grazed birches are killed by wood decaying fungi, such as *Inonotus obliquus*, *Phellinus igniarius* and *Piptoporus betulinus* (Yamaguchi 2002). This type of damage was common in Finland, so many birch hybrids were developed and examined for their resistant capacity against hares (Rousi et al. 1996).

In the year 2000, there was serious damage to adult 100 year-old birches in several regions of Hokkaido. It was considered to be the after-effects of grazing by the royal moth (*Caligula japonica*) (Ohno et al. 2003). The birch usually develops secondary shoots after the early leaves are grazed by the moth. Although the Monarch birch prefers moist soil conditions, the year was unusually dry so most secondary leaves died which may be attributed to the high susceptibility to water stress during summer when the secondary developed leaves have not fully matured. Water desiccation tolerance of the secondary developed leaves was lower than other mature leaves (Ohno et al. 2003). Consequently, the grazed birch dies since there are no leaves to complete photosynthesis.

The other important form of defense against herbivores is mechanical protection, such as toughness, the presence of trichome, etc. (e.g. Orcutt and Nilssen 2000, Peter and Shanower 2001). Trichome on the leaf surface, makes it difficult for insect larvae to bite the leaf or walk upon it. The presence of trichome in the seedlings of three birch species (*Betula ermanii*, *B. maximowicziana* and *B. platyphylla* var. *japonica*) was

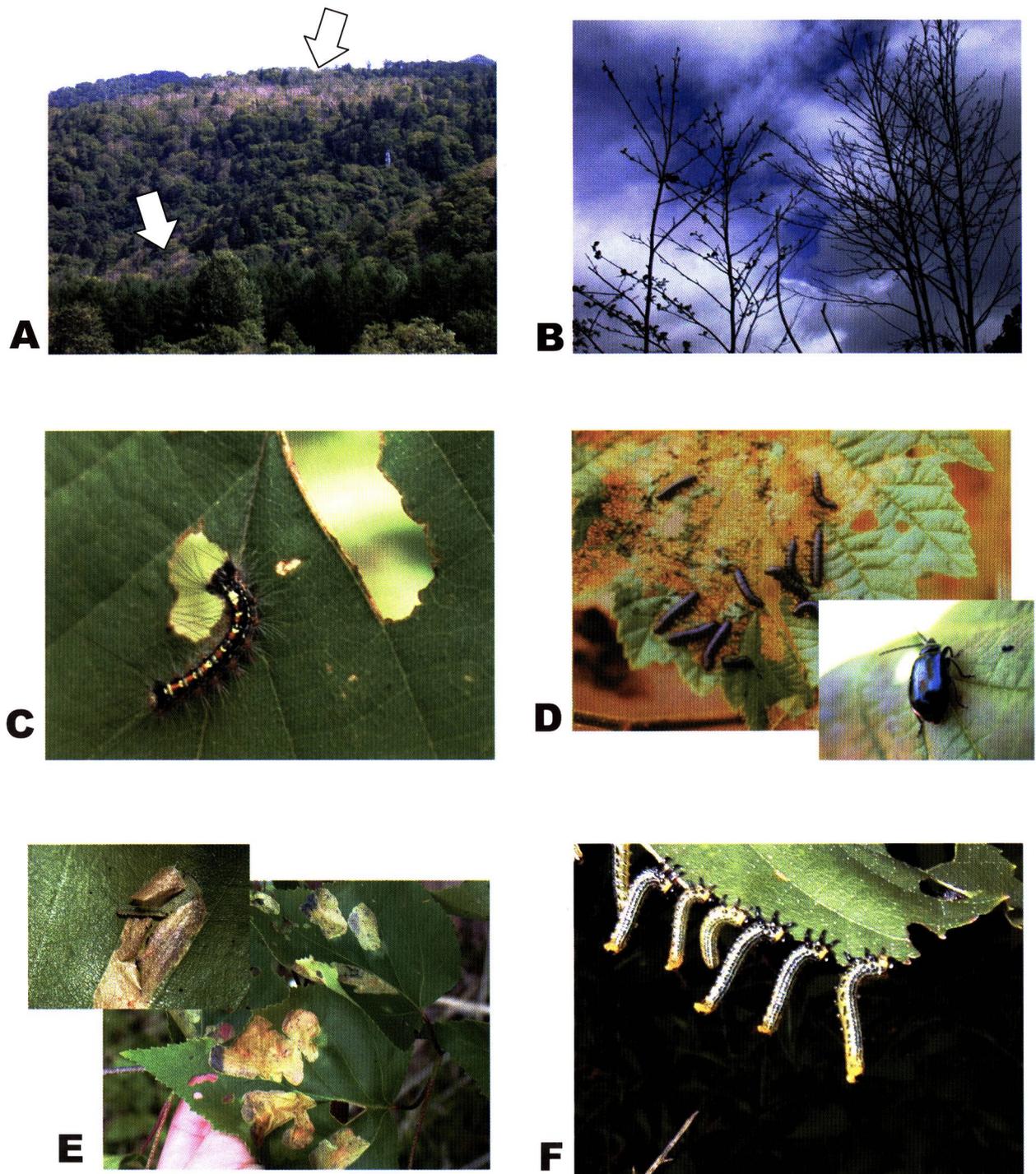


Photo. 1.

- A: Damaged mixed birch-alder stand in north Hokkaido (Nakagawa Experimental Forest of HUF, FSC).
 Arrows indicate the damaged stands.
- B: Monarch birch (left) after grazing by gypsy moth and mountain alder (right) by leaf beetles.
- C: Gypsy moth (*Lymantria dispar*) attacking a white birch leaf.
- D: An alder leaf after grazing by leaf beetle (*Agelastica coerulea*) and its adult stage.
- E: Miner attacking a white birch leaf (species unknown).
- F: A type of sawfly grazing on a mountain birch leaf.

markedly larger in early leaves but not in late leaves of *B. ermanii* and *Bplatyphylla* var. *japonica*. In contrast, only *B. maximowicziana* maintained a high trichome density in late leaves (Matsuki *et al.* 2003, Matsuki *et al.* 2004). Based on chemical analysis of both early and late leaves of the three birch species, the amount of condensed tannin in late leaves of *B. maximowicziana* is relatively smaller than the other two species, however, the trichome of its leaves may act as compensational defense.

Of course, trichome on leaf surface can increase the reflectivity of leaf and therefore reduce leaf temperature in high light conditions. This may help in increase the photosynthetic rate (Ehleringer and Björkman 1978). Therefore, the effect of trichome on herbivore which may not be the selective factor determining the way of improving photosynthetic function.

4. Defense characteristics of deciduous trees

In general, the contents of defensive chemicals are affected by not only by soil fertility, but also by the growth phase of the plant life cycle. This can be understood by applying the hypotheses of GDB (growth/differentiation balance; there is a physiological trade-off between plant growth and production of defense chemicals because both originate from the same photosynthetic products) (Lerdau *et al.* 1994) and CNB (carbon/nutrient balance; with nitrogen limitation in plants, plants can produce more carbon-based secondary defense chemicals with the use of the extra-carbon) (Bryant *et al.* 1983, Haukioja and Honkanen 1997, Kamata 1999).

Before leaf shedding in autumn, plants recycle foliar nitrogen for the next year's growth. Once leaves are grazed by herbivores, plants suffer from a shortage of nitrogen, which also creates a decrease in photosynthetic production. With grazing, damaged leaves have usually high C/N ratio and shortage in nitrogen. Under this imbalance of C/N ratio, these plants produce carbon-based secondary compound, that is the central idea of the CNB hypothesis.

Based on an evolutionary point of view, slow growing plants may allocate photosynthates more to defense chemicals when they are grown under limited nutrient conditions (Resources available hypothesis; in short RAH). Therefore, GDB hypothesis may include CNB hypothesis and RAH (Hartley and Jones 1997). These hypotheses also predict that the characteristics and quantity of leaves herbivores use as food are altered with changes in the environment. For instance, feeding on leaves grown in high CO₂ retards the growth of herbivores or kills them (Fajer *et al.* 1991, Lincoln *et al.* 1993).

The defense characteristics of plants change as the seasons progress and with the stimulation of grazing of herbivores. However, these characteristics are strongly dependent on species-specific traits (Lindroth 1995). Therefore, as baseline data for forest conservation and protection, we should summarize the defense characteristics of representative tree species under changing environments.

4.1. Defense traits in successional forest tree species

In general, early successional conifer species usually have higher susceptibility to several kinds of insects, chewer, sucker, etc. (Furuta 1992). The effect of grazing on tree survival depends on the degree of grazing and leaf habit, namely deciduousness or coniferousness. When over 70% of the leaves of evergreen trees, such as Japanese red pine (*Pinus densiflora*) are grazed by herbivores, the tree dies since evergreen foliage organs acts as both photosynthetic and storage organs. This is not the case for deciduous trees, such as Japanese larch (*Larix kaempferi* = *L. leptolepis*) or Siebold's beech (*Fagus crenata*) (Yokota *et al.* 1978). A typical example is found in the forest canopy of Siebold's beech, in which the canopy is sometimes denuded due to the grazing by beech caterpillar (*Quadricalcarifera* = *Syntypistis punctatella*) larvae, but the trees can usually survive (Kamata 1999, Kamata 2000).

The resistant capacity of tree species against herbivores is reflected by the allocation pattern of photosynthates (Mooney and Gulmon 1982), even though the synthesis pathways of phenolics and terpenoids are different. Tree species show specific patterns of shoot development and photosynthetic traits. For instance, alder growth is classified as an indeterminate growth type and is less dependent on storage materials with small amounts of condensed tannin. In contrast, beech is classified as a determinate growth type and uses storage materials for the next season's growth. Beeches usually contain large amounts of defensive chemicals such as phenolics (Kamata 1996, 1999, Koike *et al.* 2003b).

Since leaf longevity in slow-growing species or late successional species is longer, it is believed that the defense capacity of fast-growing species, i.e. early successional species is less than that of the late variety (e.g. Coley *et al.* 1985, Jones and Coleman 1991). However, the amount of foliar defense chemicals is not always reflected by leaf longevity. For example, leaf longevity of *Carpinus cordata* is relatively long, but the amount of total phenolics and condensed tannin is smaller than that of white birch with a shorter leaf lifespan (Koike *et al.* 2001). Ash (*Fraxinus mandshurica* var. *japonica*) has a relatively greater leaf longevity, but with an insignificant amount of condensed tannin (Koike *et al.* 2003a). Therefore, a plant's herbivore tolerance and the after-effects of grazing are considered to be species-specific traits. We should further examine the potential capacity of woody plants' defenses against herbivores in order to conserve forest ecosystems using fewer insecticides.

After grazing, most tree species do not die, but will change their foliar chemical and/or mechanical structure. Amount of defense chemicals of healthy leaves is usually not large because synthesis of phenolics and tannin is costly as comparing with damaged leaves (Waterman and Mole 1994, Schoonhoven *et al.* 1998, Pickett *et al.* 1999). Plants usually produce defensive chemicals after grazing by herbivores, i.e. "Induced defense." In following section, we discuss several examples of induced defense in

woody species.

4.2. Changes in foliar chemical composition following defoliation

When we cut one half of the lamina of three species of willow leaves (*Salix miyabeana*, *S. pet-susu* and *S. sachalinensis*) with scissors in mid May, the light-saturated net photosynthetic rate (P_{sat}) of the remaining leaves at early August increased significantly to 1.3 times that of the control leaves (P<0.01) (Fig. 1) (Koike *et al.* 2003b). There was also an increase in leaf nitrogen content. These seedlings had been planted the preceding year and treated with fertilizer after they were established in a nursery. However, there was no statistical difference in the growth among the three

willow species treated with a lamina cut in early flushed leaves. Instead of cutting treatments on leaves, these responses were accelerated by the application of a balanced fertilizer (condensed Hyponex liquid fertilizer diluted 1000 times) (Koike *et al.* 2003b). The increment of biomass and tree height of willow seedlings was only found in the balanced fertilizer treatment because the longevity of leaves flushed in spring was relatively short in the control.

The same experiment was carried out for Siebold's beech (Koike *et al.* 2003b). No clear increase of P_{sat} in the remaining leaves was found. However, the increment of diameter of the treated seedlings was smaller than that of the control. The growth increase of seedlings treated in fertile conditions was detected in

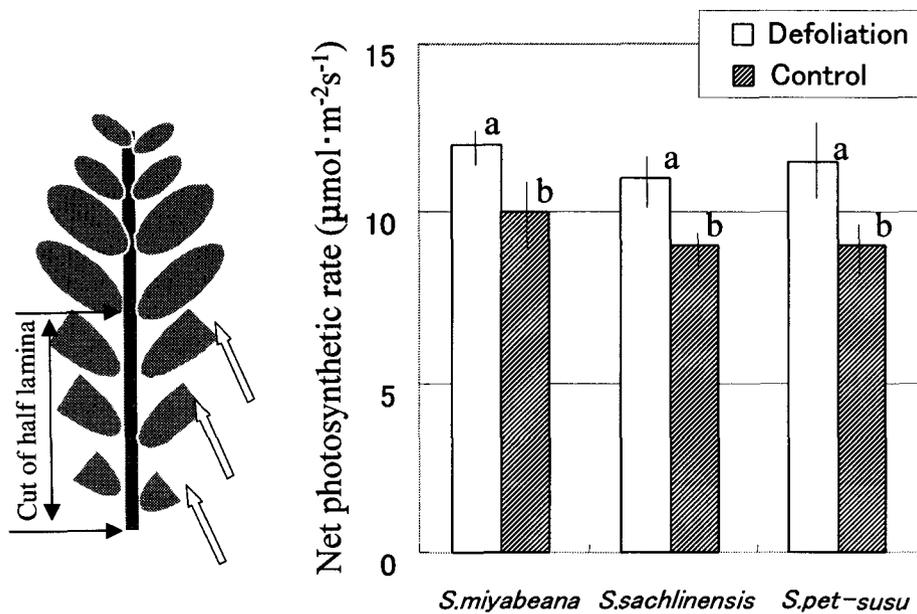


Fig. 1. Effect of defoliation on the net photosynthetic rate (P_n) of three willow species. After Koike *et al.* (2003b). Vertical bars show the standard error. Different alphabet means statistical significant (P<0.01). Defoliation was made at mid May (in Tokyo) when no current shoots were elongated. Half-length of lamina of all leaves was cut by scissors (arrows indicate the treatment position). P_n of cut leaves increased slightly with decreasing SLA (cm²·g⁻¹) and increasing leaf nitrogen content.

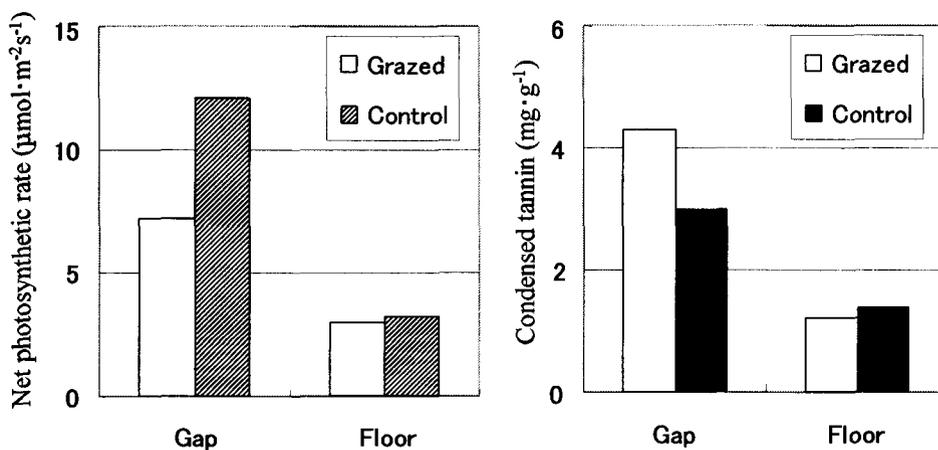


Fig. 2. Effects of grazing damages caused by moth larvae on the net photosynthetic rate (P_n) and the amount of condensed tannin in oak seedlings. After Nabeshima *et al.* (2001).

the second year after the treatment. The defense chemicals increased in the uncut leaves of unfertilized beech but not in leaves that had been cut with scissors.

Once leaves of Siebold's beech are grazed, the production of condensed tannin continues for the following three years (Kamata 1999). When plants would be grazed by herbivores, plants usually change morphology, qualities and quantities of defense chemicals and the composition of foliar carbon and nitrogen. Changes in a plant's chemical defense following grazing by herbivores, which is usually influenced by growth conditions, may affect the composition and interaction between or among plants and herbivores in nature.

A compensational increase of Psa was observed with the partial defoliation of birch (*Betula pendula*) leaves with scissors (Ovaska et al. 1993a,b). There was also an increase in Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase). The birch seedlings that had leaves cut with scissors had an increase in LMA (leaf mass per area; g.m⁻²) but not in the content of defense chemicals. The important role of elicitor has been studied in relation to induced defense (Korth and Dixon 1997, Schoonhoven et al. 1998, Karban and Baldwin 2001). Induced defense prior to gene expression is usually observed with the presence of larva saliva (Korth and Dixon 1997). To test the role of elicitor, a grazing experiment on oak seedlings (*Quercus mongolica* var. *grosseserrata* = *Q. crispula*) was carried out with the use of three kinds of larvae of Lepidoptera (Nabeshima et al. 2001). Under gap condition in a secondary forest of deciduous broad-leaved trees, the net photosynthetic rate (Pn) of oak leaves grazed by moth larvae decreased significantly while the amount of condensed tannin markedly increased (P<0.01). There was no clear increase found in the seedlings grown on the forest floor (Fig. 2).

In practical forestry, an introduced species usually suffers from several kinds of grazing and disease, as seen in larch plantations. In the past, insecticides were applied to regulate the populations of insect herbivores. However, further studies are needed in regulated and in natural conditions to predict the interactive-web of plants and insects.

5. Specialist vs. generalist

The uncertainty of plants as resources for insect herbivores may regulate the impact of grazing or the population dynamics in grazers. Therefore, insect herbivores cannot fully graze foliar organs because of defense, temporal and special variation in quality (Ohgushi 1992, Hara 1994, Masaka and Hara 2000). Specialists (or monophagy) usually use a host-specific signal as a positive indicator of host suitability. Such insect herbivores have relatively specialized receptors for detecting the special chemicals of host plants, especially secondary chemicals. As a result, specialists can monopolize the plant with increasing the concentration of chemical cues.

Specialists can graze selectively specific plants. For example, most sawflies cannot eat the leaves of mountain poplar (*Populus maximowiczii*) containing

the precursor of salicylic acid. However, the poplar sawfly, as a specialist, (*Chrysomela populi*) can eat the leaves of *P. maximowiczii*. The grazing activities of the sawfly change drastically from year to year because of large differences in the content and quality of defensive chemicals in *P. maximowiczii*. Similar events were reported for the shoot-bring sawfly (*Pleroneura piceae*) attacking young shoots of Sakhalin spruce (*Picea glehnii*). Damage caused by the sawfly depends on the progress of shoot development, i.e. the phenology of shoots. The early shoot-flush individuals can avoid boring damage by the sawfly (Masaka and Hara 2000). After a few years, late shoot-flush individuals will be destroyed by sawfly infestation.

The responses of specialists to foods with slightly different foliage quality will vary which will change the interspecific and community structure of insect herbivores (Jones and Coleman 1991). Similarly, the selection of plants as food by generalists (or polyphagous herbivores) is usually dependent on the specific growth conditions of host plants. Generalists tend to use ubiquitous signals and plant-species specific characteristics often function as negative indicators of host suitability. The effect of food quality for adult herbivores and the phenological condition on the growth and development of offspring may have a critical role on the fitness and stability of a population. However, the fluctuations of phenology and growth conditions of host plants are not stable but vary temporally. In fact, particularly toxic or inhibitory compounds in a given plant may be processed inefficiently, leading to greater decreases in performance compared with specialists.

6. How to increase defense levels; a challenge for bottom-up regulation

6.1. Introduction to hybrid larch

Japanese larch was regarded as a promising tree for timber production because it has high photosynthetic rate (Fry and Philips 1976) but not considered a C4 plant (Richards and Teeri 1982). However, Japanese larch has high susceptibility to grazing by voles and to infection with shoot blight (Koike et al. 2000). Improving growth traits of Japanese larch to resist vole grazing and shoot blight disease started in 1938 at Hokkaido Forestry Experiment Station (Hokkaido Regional Government 1987, Koike et al. 2000). Vole damage (mainly by red-backed vole; *Clethrionomys rufocanus bedfordiae*), had been especially destructive. In 1954, a high resistant hybrid larch was discovered by chance at the Tokyo University Forest located in central Hokkaido. Even though initially, the goals of the breeding program were to improve the resistance to vole grazing and the shoot blight disease (Fig. 3), the efforts have improved not only the resistant capacity to many kinds of stress but have also improved timber quality.

Based on screening tests, we found that Dahurian larch (*Larix gmelinii*) had a higher resistance to both vole grazing and shoot blight disease, especially the trees originating from the Kurile Islands (but not from Sakhalin Island) (e.g. Kuromaru 1995). Recently,

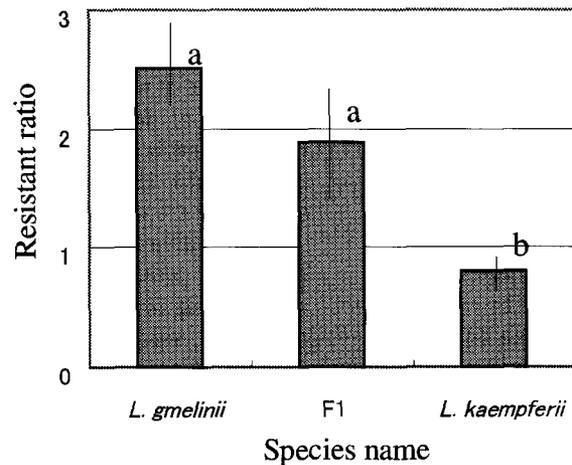


Fig. 3. Breeding target was to improve the resistant capacity against vole grazing and disease. After Koike *et al.* (2000). Different alphabet means statistical significant ($P < 0.01$). Vertical bars show the standard error.

Orihashi *et al.* (2003) found a high capacity in F1 hybrid larch to withstand bark stripping by Sika deer (*Cervus nippon yezoensis*). In addition, Dahurian larch has greater resistance to frost than the Japanese larch. This low temperature strength in Dahurian larch can be attributed to its phenological traits, namely early flush and early shedding of needles (Hamaya *et al.* 1968, Koike *et al.* 1988). The F1 hybrid larch was produced by crossing a Dahurian larch, from the Kurile Islands, with a Japanese larch. The chloroplast was inherited paternally from Japanese larch (Shmidt *et al.* 1987) and the other growth characteristics, such as wood density and high resistance capacity were inherited maternally from the Dahurian larch (Hokkaido Regional Government 1987). This successful development of F1 hybrid larch, capable of resisting several biological stresses, is an example of bottom-up regulation between plant-animal interactions.

6.2. Practical use of F1 hybrid larch

Recently, we have used this F1 hybrid larch as the planting stock for all of Hokkaido Island. Most growth traits display a median between the Dahurian and Japanese larch (Hokkaido Regional Government 1987, Kuromaru 1995, Orihashi *et al.* 2003). The resistance to the Red-backed vole was the most important characteristic of the F1. The health of larch plantations in Hokkaido has been maintained by the introduction of the F1 hybrid. However, the mass production of F1 seedlings has been difficult because such heterosis is only present in the first generation. To produce high quality F1 seedlings, we created many seed orchards in Hokkaido. However, the seed production rate of the F1 has been limited to a maximum of 60% because of natural open pollination (Kuromaru and Satoh 1986). We then introduced a micro-propagation method of apical shoot meristems for mass production of F1 seedlings. The result was called a “Gream” from combining the English words “green” and “dream” (Kuromaru and Satoh 1986; Kuromaru 1995).

For nursery practices, after germination, seedlings of the F1 can grow roots more quickly at lower temperatures (ca. 7 °C) and under infertile conditions compared with seedlings of Japanese larch (Prokushkin *et al.* 2001, Qu *et al.* 2003). Even though there have been many technical difficulties, we have succeeded in keeping the forests strong with the F1.

7. Factors affecting the production of defense chemicals

7.1. Growth characteristics of tree species

Most early successional tree species produce secondary substances intensively, i.e. defense chemicals, after the cessation of active vegetative growth (Kamata 1999). Seedlings of late successional tree species, e.g. maple and beech, flush at the beginning of growing season and are apt to die when most of their leaves have been grazed by herbivores because a secondary flush of tree seedlings rarely occurs on a shady forest floor. In general, to avoid grazing damage, these late successional plants have high structural and chemical defense capacities because their longer leaf lifespan makes it necessary for them to be more resistant to grazers compared to early successional species (Coley *et al.* 1985, Koike *et al.* 2003a).

The growth responses to fertile conditions are usually accelerated for early successional species but not for late successional ones. What kinds of factors affect the production of defense chemicals in different successional traits of trees? Based on several studies (e.g. Kamata 1999, Mooney and Gulmon 1982), the photosynthetic rate of early successional tree species increases with an increase in the content of foliar nitrogen and photosynthates are mainly allocated to growth but not to defense. As a result, the content of defense chemicals, such as total phenolics and condensed tannin decreases with an increase in soil fertility. These ideas are explained through the CNB hypothesis as stated previously in this review paper and Hikosaka *et al.* (2003).

The high content of defense chemicals in long-lived leaves of late successional tree species was also found. A positive correlation was found between foliar C/N ratio and defense chemicals (e.g. total phenolics, condensed tannin) in six deciduous broad-leaved tree seedlings raised under two factorial combinations of PPF and nutrient levels (Fig. 4) (Koike *et al.* 2003a,b). Except for oak seedlings (*Quercus mongolica* var. *grosseserrata*), most deciduous broadleaved tree seedlings grown in shady low nutrient environments experienced a marked increase in the content of total phenolics but not in condensed tannin. The amount of defensive chemicals in oak increased with an increase in soil fertility. Only trace amounts of condensed tannin can be found in the leaves of ash (*Fraxinus mandshurica* var. *japonica*). However, based on the examination of six species, such as white birch (*Betula platyphylla* var. *japonica*), basswood (*Tilia japonica*), ash, oak, maple (*Acer mono*) and elm (*Ulmus davidiana* var. *japonica*), there was no clear relationship between leaf longevity and defense chemical content (Koike *et al.* 2003a).

Again, when carbon gain is limited (i.e. under shading) relative to nutrient availability, the resource availability hypothesis, which is based on the carbon-nutrient balance (CNB) hypothesis, predicts a decline in the allocation of carbon-based secondary metabolites (Bryant *et al.* 1985). In contrast, the allocation of nitrogen-based secondary metabolites increases. Thus, when plants are facing nitrogen deficiencies, the allocation of carbon-based secondary compounds should increase because surplus carbon may be transferred to defense chemicals. However, production of nitrogen-based secondary compounds should decrease (Bryant *et al.* 1985, Jones and Coleman 1991, Hartley and Jones 1997).

It is thought that there may be a trade-off relationship

between growth and defense capacity not only within a species but also among species in certain plant groups. There was a positive correlation between leaf C/N, as an indicator of soil fertility through plant growth, and the amount of total phenolics and condensed tannin (i.e. allocation to defense) in six species raised under two factorial combinations of light and nutrients (Koike *et al.* 2003a,b). However, the correlation was not strong among the six species' seedlings.

In an individual, there should be a trade-off between growth (= protein synthesis through Acetyl CoA) and synthesizing defense chemicals (e.g. synthesis of tannin, coumarins, etc.) because both syntheses originate from phenylalanine through a shikimic acid pathway (Waterman and Mole 1994, Orcutt and Nilsen 2000). In contrast, there is no relationship between the amount of terpenoid and growth in Scot pine (Honkanen *et al.* 1999), which may be attributed to a metabolic mevalonate pathway. Terpenoids come from Acetyl CoA via mevalonate but not shikimic pathways (Waterman and Mole 1994).

7.2. Effects of increasing CO₂ and pollutants

Recently, atmospheric CO₂ is increasing yearly with an accompanying increase in temperatures. This will surely bring changes in both the life cycle of insect herbivores (Bale *et al.* 2002) and the composition of defense chemicals in leaves (Lincoln *et al.* 1993, Lindroth 1995, Roth *et al.* 1998, Saxe *et al.* 1998, Yin 2002). In fact, the carbon concentration of leaves and C/N ratio of leaves in high CO₂ increases with decreasing nitrogen concentration (Docherty *et al.* 1997, Roth *et al.* 1998, Koike *et al.* 2001, Koike unpublished). This tendency may be the specific responses of individual tree species. The amount of total phenolics and condensed tannin of white birch and Japanese larch was ca. 60% less than those of Siebold's beech,

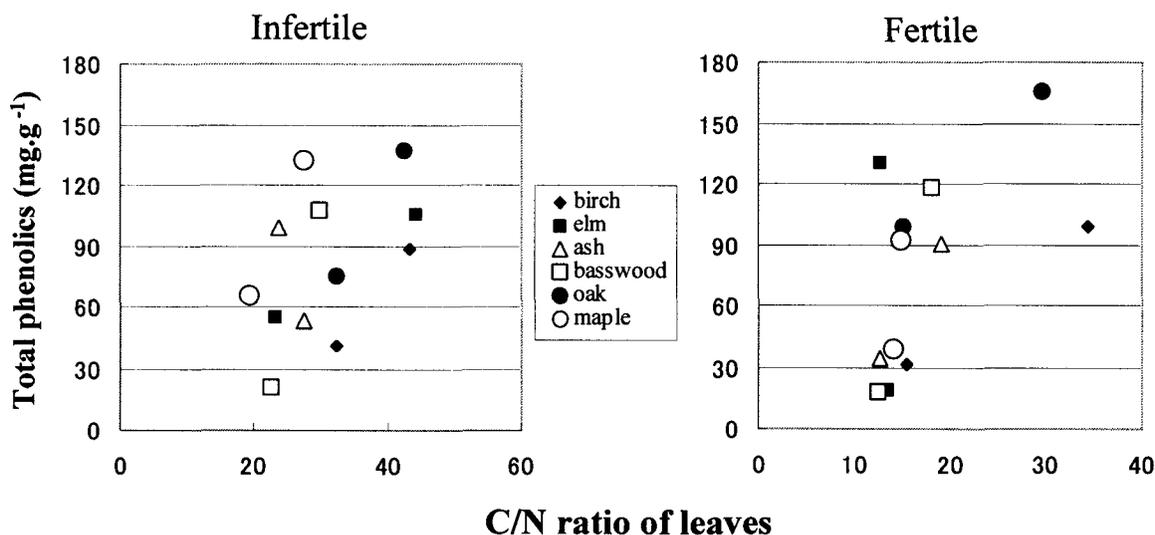


Fig. 4. A positive correlation was found between foliar C/N ratio and defense chemicals (e.g. total phenolics and condensed tannin) in 6 deciduous broad-leaved tree seedlings raised under two factorial combinations of PPF and nutrient levels. From Koike *et al.* (2003a,b). Under relatively high PPF, Pn increases which also increases the amount of carbon-based secondary compounds, such as total phenolics and condensed tannin. This relationship is affected by soil fertility.

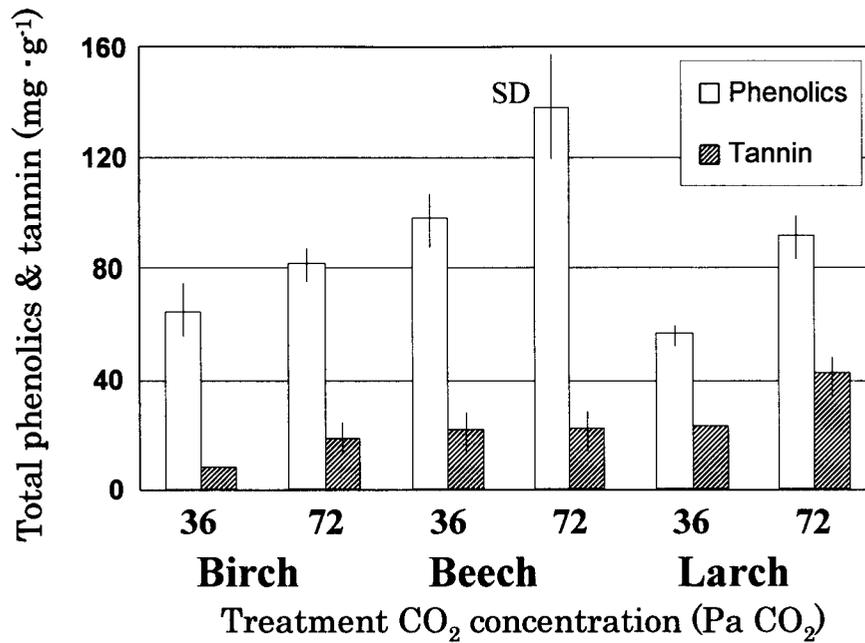


Fig. 5. Total phenolics and condensed tannin in foliage of birch, beech and larch seedlings raised under ambient and elevated CO₂ (From Koike *et al.* 2001, and larch from unpublished data of Koike).

independent of an increase in CO₂. However, in high CO₂ environments, Japanese white birch (*Betula platyphylla* var. *japonica*) and Japanese larch increased both total phenolics, and condensed tannin, in contrast, Siebold's beech increased only total phenolics but not condensed tannin (Fig. 5). Under elevated CO₂, Finnish white birch (*Betula pendula*) increased flavone aglycones and decreased individual glycosides, cinnamoylquimic acids and (+)-catechin. There was no significant effect of CO₂ and temperature on the phenolic concentration in leaves and stem, while the number of resin drops in the shoot top, which makes it resistant to hares, (Rousi *et al.* 1996) showed significant interaction (Kuokkanen *et al.* 2001).

Sugar maple, aspen, birch and red oak, four species native to North America (aspen- *Populus tremuloides*, paper birch- *Betula papyrifera*, red oak- *Quercus rubra*, sugar maple- *Acer saccharum*), the leaf nitrogen concentration in high CO₂ treatments decreased, however, aspen, birch and red oak showed increased total phenolics and condensed tannin. The sugar maple is the species, which increased only condensed tannin but not for total phenolics (Lindroth 1995).

The body mass of some larvae is retarded when they feed on leaves raised in high CO₂ environments (Fajer *et al.* 1991, Roth *et al.* 1998). Bioassay shows that this tendency is not always found in all species of insect herbivores, but there are very few exceptions (Docherty *et al.* 1997). In fact, the growth rate of the larvae of several kinds of moth (e.g. gypsy moth, Luna moth, forest tent caterpillar, etc.) feeding with leaves grown high CO₂ showed specific patterns (e.g. Lindroth 1995). Therefore, we should further examine the interactions between herbivores and plants grown in high CO₂ environments.

Moreover, in the presence of high CO₂, defoliation

reduced the amount of water content and nitrogen in aspen (*Populus tremuloides*) but had no effect on primary metabolites in maple (*Acer saccharum*). Defoliation treatment also increased the accumulation of tannin and phenolics in aspen but not in maple. Larvae fed leaves from the enriched CO₂ or defoliated treatments showed reduced growth compared with forest tent caterpillar (*Malacosoma disstria*) fed leaves from the ambient CO₂ treatment. However, the patterns of larvae were host species-specific (Lindroth 1995, Roth *et al.* 1998). Even in the same genus of *Betula*, the composition of secondary chemicals differed greatly among species in ambient CO₂ (Shen *et al.* 2000) and elevated CO₂ (Matsuki *et al.* 2003). Therefore, we should research the numerous combinations of plants and insect larvae as material for a bioassay to predict future changes in the balance of host and parasite interactions in forest ecosystems. We must also focus on plant-insect interactions under polluted conditions (Docherty *et al.* 1997). For instance, ozone (O₃) damaged-trees were less resistant to insect attack because of a reduced rate of resin flow and exudation. Of course, the effect of O₃ on herbivores is difficult to predict, especially for aphids. Further studies will be needed in regulated and in natural conditions to predict the web of interactions between plant and insect herbivores.

8. Further consideration of bottom-up regulation as conclusion

The philosophy of top-down regulation emphasizes the role of natural enemies for controlling the population of insect herbivores and consequently the stabilization of forest ecosystems (Price 1992). With progress in the detailed analysis of the interactions between plants and animals (e.g. insect herbivores), the

idea of bottom-up regulation, based on findings in nature, is also a way to understand ecosystems (Hartley and Jones 1997, Ohgushi 1999).

Plants resources, such as the foliage of woody plants, are not always suitable food for insect herbivores because they change temporally and spatially in quality and quantity (e.g. Hunter *et al.* 2001). This change occurs primarily in foliar phenology or masting events. In addition, the amount of foliage biomass for grazing is usually estimated to be smaller than that of actual foliage biomass due to several defensive traits in woody plants. Of course, both regulation systems act tandem to stabilize plant-animal communities, which are strongly related to ecosystem structure and environmental conditions.

Although, plants produce several defense chemicals and for their own physical protection, such as trichome and toughness, they cannot completely avoid the grazing damage of insect herbivories. There is so-called "specialists" who have developed the ability to detoxify the defensive chemicals. Producing defense chemicals requires relatively large amounts of photosynthates compared to other growth compounds (Schoonhoven *et al.* 1998, Pickett *et al.* 1999, Orcutt and Nilsen 2000). Photosynthates are allocated to both growth and defense. As a result, the defensive level of plants fluctuates largely (temporally and spatially) through the seasons and the plant's life as well. As previously documented (Chapter 6), the defense levels and traits of plants differ greatly among species and individuals. Mechanical cutting of several deciduous broad-leaved tree species stimulated physiological, chemical and physical responses similar to those experienced by these species when grazed by herbivores. Induced defense was only found with the presence of herbivore saliva. These types of interactions between plants and herbivores should be studied using long-term ecological observation and monitoring in hopes of finding ways to strengthen the forest's defenses against several herbivores.

Under polluted air conditions, the vigor and health of plants may decrease and the susceptibility to herbivorous insects and bark beetles will increase (Docherty *et al.* 1997). The production of resins in conifers, an important function in defense, decreased in polluted regions. However, information on plant defense traits under polluted conditions is still very limited. Further studies will be needed to understand the interaction between plants and herbivores in this type of environment.

We have, through the use of insecticides and herbicides, severely damaged our natural environment. We should understand the potential capacity of the natural defenses of woody plants against herbivores in order to conserve forest ecosystems using less chemical assistance. We should keep our forests healthy and vigorous to face the coming changes in atmospheric conditions, such as the global increase in CO₂.

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