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journal or publication title	Proceedings, International Symposium of the Kanazawa University 22st-Century COE Program
volume	1
page range	402-405
year	2003-03-16
URL	http://hdl.handle.net/2297/6439

Effects of Defoliation on Defense Characteristics in Leaves of Deciduous Broad-Leaved Tree Species in Changing Environment

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Abstract- Effects of defoliation on the defense responses of deciduous broad-leaved trees were summarized from the viewpoint of forest ecosystem stability. Defense chemicals of leaves (condensed tannin and total phenolics) increased with a rise in foliar C/N. 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 defense chemicals of 3 species (oak, elm and maple) was larger than in ash and alder. A potential defense capacity in forest trees against herbivores is discussed in changing environment.

I. Introduction

The role of natural enemies on the stability of a forest ecosystem has emphasized the concept of "top down" regulation [1, 2]. With the progress in the study of the interactions between plants and herbivores [3, 4, 5] and in the analysis of foliar chemicals [6, 7, 8], defense capacities of plants are seen as a "bottom up" process. This has led to a new understanding of the web of interaction between plants and herbivores in a forest ecosystem [1].

In general, the contents of defense chemicals are affected by not only soil fertility, but also by the growth phase of the plant life cycle, which can be understood by applying the GDB (growth/differentiation balance) [9] and CNB (carbon/nutrient balance) hypotheses [10]. 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 [11, 12].

The defense characteristics of plants change as the season's progress and with the stimulation of grazing of herbivores. However, these characteristics are strongly dependent on species-specific traits [13]. Therefore, as baseline data for forest conservation and protection, we should summarize the defense characteristics of representative tree species under changing environment.

II. Defense Characteristics in Successional Forest Tree Species

In general, nearly 10% of foliage of forest trees is usually consumed as secondary production, i.e. grazing activities of herbivores, however, it rarely results in tree mortality. In general, early successional tree species usually have higher susceptibility to several kinds of insects [14].

Table I
Number of three kinds of insects on representative conifers with different growth traits

Growth	Species	Sucker	Chewer	Beetle	Total
Fast	<i>Pinus densiflora</i> <i>P. sieboldii</i>	26	19	32	77
Med-	<i>Cryptomeria</i> <i>japonica</i>	11	15	10	36
Slow	<i>Chamaecyparis</i> <i>obtusa</i>	5	7	9	21

Data are cited from Furuta [14]

The effect of grazing on tree survival depends on the degree of grazing and leaf habit, namely deciduousness or evergreenness. When over 70% of the leaves of evergreen trees, such as Japanese red pine (*Pinus densiflora*) are grazed by herbivores, the tree dies because the foliage of evergreen trees acts as both photosynthetic and storage organs. This is not the case for deciduous trees, such as Japanese larch (*Larix kaempferi*) or Siebold beech (*Fagus crenata*) [15]. A typical example is found in the forest canopy of Siebold beech, which sometimes becomes blighted because of the grazing of beech caterpillar (*Quadralcarifera punctatella*) larvae but the trees survive [4].

The resistant capacity of tree species against herbivores is reflected by the allocation pattern of photosynthates. For instance, the growth of alder is classified as an indeterminate growth type and is less dependent on storage materials with small amount of condensed tannin. In contrast, beech is classified as a determinate growth type and uses storage

materials for the next season's growth. Beech usually have large amount of defense chemicals.

Since leaf longevity in late successional species is longer, it is believed that the defense capacity of early successional species is less than that of late successional species. However, the amount of foliar defense chemicals is not always reflected in leaf longevity. For example, leaf longevity of *Carpinus cordata* is relatively long, but the amount of total phenolics and condensed tannin is smaller than white birch with a shorter leaf life span. Ash (*Fraxinus mandshurica* var. *japonica*) has longer leaf longevity, but with an insignificant amount of condensed tannin [7]. Therefore, a plant's herbivore tolerance and the after effects of grazing are considered to be species-specific traits. Therefore, we should understand the potential capacity of woody plants defense against herbivores in order to conserve forest ecosystems without using further insecticides.

The other important form of protection is the mechanical, such as toughness, the presence of trichome, etc. The presence of trichome, which may act as physical and structural defense of leaves, in three birch species (*Betula ermanii*, *B. maximowicziana*, *B. platyphylla* var. *japonica*) was a markedly high in early leaves but not in late leaves of *B. ermanii* and *B. platyphylla* var. *japonica*. In contrast, only *B. maximowicziana* maintained a high trichome density in late leaves [8].

III. Factors Affecting the Production of Defense Chemicals

Most early successional tree species produce secondary substances intensively, i.e. defense chemicals, after the cessation of active vegetative growth [4]. Seedlings of late successional tree species, e.g. maple and beech, flush at the beginning of the growing season and are apt to die when most of their leaves are grazed by herbivores because a secondary flush rarely occurs in 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 longevity makes them more susceptible to grazers compared to early successional species.

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 of different successional traits of trees? Based on several studies [4, 16], 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 would decrease with an increase in soil fertility. On the other hand, the content of defense chemicals in long-lived leaves of late successional tree species w A negative correlation was found between foliar nitrogen content and defense chemicals in 6 deciduous broad-leaved tree seedlings (e.g. total phenolics and

condensed tannin)(Fig. 1) [7]. Except for oak (*Quercus mongolica* var. *grosseserrata*), most deciduous broadleaved tree seedlings grown in shady low nutrient environments experienced an increase in the content of total phenolics but not in condensed tannin. The amount of defense chemicals in oak increased with an increase in soil fertility. Only trace amounts of condensed tannin can be found in the leaves of ash. However, based on the examination of 6 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 [7].

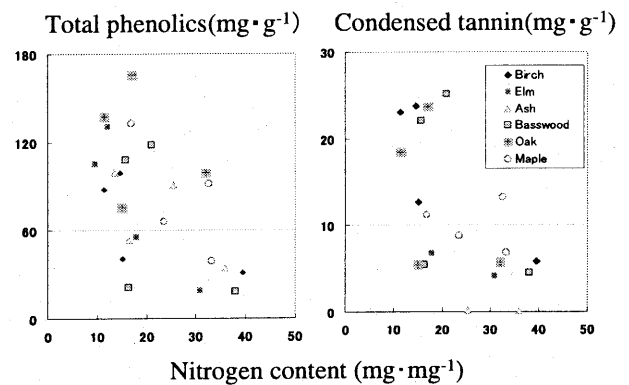


Fig. 1. Relationship between leaf nitrogen content and total phenolics or condensed tannin among 6 broad-leaved tree seedlings grown under different nutrient regimes [7].

Recently, atmospheric CO₂ is increasing yearly, which surely changes the composition of defense chemicals in leaves. In fact, carbon concentration of leaves and C/N ratio of leaves in high CO₂ increase with decreasing nitrogen concentration [17, 18]. Moreover, this tendency may be specific responses of trees, e.g. in high CO₂, white birch and Japanese larch (*Larix kaempferi*) increased both total phenolics and condensed tannin, in contrast, Siebold beech increased only total phenolics but not condensed tannin. Among four species native to North America, except for sugar maple, aspen, birch and red oak increased total phenolics and condensed tannin. Sugar maple increased only condensed tannin [13]. Body weight of some larvae is retarded when they are feeding with leaves raised in high CO₂ [11]. However, growth rate of larvae of several kinds of moth (e.g. gypsy moth, Luna moth, forest tent caterpillar etc.) feeding with leaves grown at high CO₂ was showed specific patterns. Therefore, we should examine further the interaction between herbivores and plants in high CO₂.

IV. Foliar Chemical Composition Following Defoliation

When we cut one half of the lamina of willow leaves with scissors in early July, the light saturated net photosynthetic rate (P_{sat}) of the remaining leaves increased significantly 1.3 times higher than that of the control leaves (P<0.01) (Fig.

2) [19]. 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.

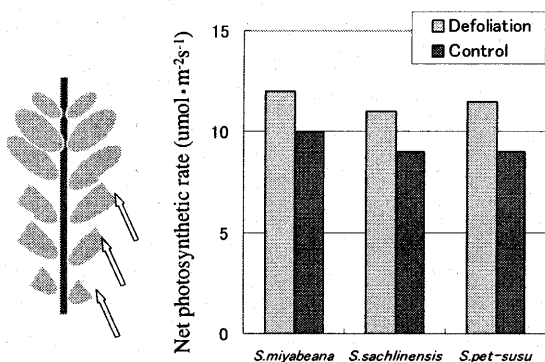


Fig. 2. Effect of defoliation on the net photosynthetic rate of three willow species [19].

Arrows indicate the position of cut lamina. After the cut treatment with sensors, leaf mass area increased of the rest part of leaf.

However, there was no statistical difference in the growth among the three willow species treated with lamina cut in early flushed leaves (*Salix miyabeana*, *S. pet-susu*, *S. sachalinensis*). These responses were accelerated by the application of a balanced fertilizer (condensed Hyponex liquid fertilizer diluted 1000 times) [19].

However, the increment of biomass and tree height of willow seedlings was only found with the balanced fertilizer treatment because the longevity of leaves flushed at spring was relatively short in the control. The same experiment was carried out for Japanese beech (*F. crenata*). No clear increase of Psat in the remaining leaves was found. However, the increment of diameter of the treated seedlings was smaller than that of the control. The growth of seedlings treated in fertile condition was detected in 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.

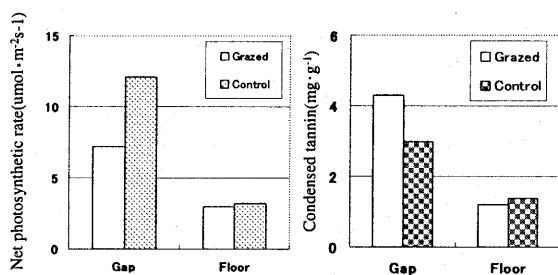


Fig. 3. Effects of grazing damages caused by moth larvae on the net photosynthetic rate (Pn) and the amount of condensed tannin in oak seedlings. After Nabeshima et al. [23]

Under gap condition, Pn of leaves grazed by moth decreased significantly while the amount of condensed tannin markedly increased ($P < 0.01$).

A compensational increase of Psat was observed with the partial defoliation of birch (*Betula pendula*) leaves with scissors [20, 21]. 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; $\text{g} \cdot \text{m}^{-2}$) but not in defense chemical content.

The important role of elicitor has been studied in relation to induced defense [6, 22]. Induced defense is usually observed with the presence of larva saliva. In fact, the defense chemical contents increased in oak seedlings with moth larva grazing [23].

Once leaves of beech are grazed, the production of total phenolics and condensed tannin continues for the following three years [4]. Plants usually change morphology, defense chemicals and the composition of foliar carbon and nitrogen when grazed by herbivores. Changes in a plant's chemical defense following the grazing by herbivores, which is usually influenced by growth conditions, may affect the composition and interaction between or among plants and herbivores.

V. Summary and Conclusions

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 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 tree's defense against several herbivores. More information of the long-term ecological studies in Hokkaido University Forests, FSC is available in the web site (<http://pc3.nrs-unet.ocn.ne.jp/~exfor/FR/>). Further contact will e-mail (tkoike@exfor.agr.hokudai.ac.jp).

Acknowledgments

We thank Drs. Y. Maruyama, M. Kitao and H. Tobita of Hokkaido research center of the Forestry and Forest Products research Institute for their kind support in the CO₂ related experiments and Mr. T. Fukui and Mr. H. Mamiya of FSC, Hokkaido University for support in nursery studies. Thanks are also due to Dr. N. Kamata and Prof. T. Ohgushi for invaluable comments on the study.

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