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## Plant Defense Characteristics and Hypotheses in Birch Species

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### Abstract

Birches employ defense when under pressure, either biotic or abiotic or both. They have at least three types of defense against herbivores, involving physical, chemical and phenological strategies, whether the defense is constitutive or induced. Leaves usually use both types of defense, whereas woody parts (stems, branches, or twigs) deploy mostly chemical defense. Other studies scarcely differentiate between proposed plant defense models such as CNBH and GDBH, and the defensive responses of birches, since there is a large variation in defensive responses. The evidence supports neither the carbon-nutrient balance (CNB) nor the growth-differentiation balance (GDB) hypothesis in birch defense, indicating that defense is genetically regulated. In our review, we may conclude that birches deploy their various defenses in parallel, since these derive from distinct chemical and physical mechanisms.

**Keywords:** Birch (*Betula*), chemical defense, physical defense, trade-off relation, proposed defense models

### Introduction

Birches (*Betula* sp.) are widely distributed in cool-temperate forests in the northern hemisphere, and are important successional woody species (Rousi *et al.* 1996, Koike 1995, Koike *et al.* 2003, Pritinen 2005). These plants are ecologically and economically significant for their wide utilization, which includes the use of their sap and use as a medicinal source; also for wooden implements (plywood, furniture, high quality paper) (e.g. Zyryanova *et al.* 2010) and for landscaping (Rousi *et al.* 2006). These uses vary with region and the native culture. As pioneer tree species, birches usually thrive after forest fires, clear cutting, or soil scarification, giving rise to birch-dominated secondary forest (Ohno and Terazawa 2005). Birch grows quickly and provides shade and habitat for wildlife. Soon after birches are growing, the cleared area will begin to regenerate as a result of the presence of other species, such as spruce, fir, or aspen (Ginsburg 2010).

Birches usually suffer from grazing by insect and mammal herbivory (Rousi *et al.* 1996), as well as attack by pathogens or fungi (Clement and Malinoski 2009). These attacks can affect the growth, reproduction, and survival capability of birches (e.g. Bryant *et al.* 1983) and sometimes lead to the death of the tree. Strong defense mechanisms are needed to ensure that these birches thrive and can be exploited.

Plants have various defense mechanisms against herbivores. Physical and chemical means are direct defenses, whereas indirect defense, such as mimicry, and non-preference defense (leaf shading or leaf color change) are other defensive strategies (Giertych *et al.* 2006).

Birches use both direct and indirect defense. The

woody parts employ mainly chemical defense against herbivores (Rousi *et al.* 1996, Laitinen 2004, Pritinen 2005), and leaves use both chemical and physical defense mechanisms (e.g. Koike *et al.* 2003, Matsuki *et al.* 2004, Matsuki 2006). Birch species, like many woody plants in temperate forests, also exhibit non preference-strategy through autumn coloration of leaves. The autumnal color of the leaves appears to be in negative correlation with damage caused by insect herbivores in the following season (Hagen *et al.* 2003).

The defenses of birches have been studied before. Some models of plant defense were developed to explain variations in plant defense against predators, such as the optimal defense hypothesis (ODH) (Riipi *et al.* 2002), the carbon-nutrient balance hypothesis (CNBH) (Bryant *et al.* 1987), the growth rate hypothesis (GRH) (Chapin 1980, Almeida-Cortez *et al.* 2004), and the growth-differentiation hypothesis (GDBH) (Herms and Mattson 1992, Glynn *et al.* 2007). Given the present increases in nitrogen deposition and atmospheric CO<sub>2</sub> concentration (Koike *et al.* 2006b,c), environmental change should be considered and its effects on defense capacity and consequently on the productivity of birch species in nature. The present review compiles information on defense in birch trees in the light of the defense models specified above. How do birches enact defense? Do defenses fit one or more of the above models?

### Types of Defense in Birches

Birches have several forms of defense against herbivores. Variation in the defense mechanism exists within and among species. Many studies have found distinct mechanisms of resistance to herbivorous insects

and mammalian pests in birch species (e.g. Rousi *et al.* 1997).

Plant defense can be categorized broadly into constitutive defenses and induced defenses (e.g. Matsuki 2003, Aoyama and Koike 2010). Within these two categories there are at least three strategies adopted by birches, namely chemical, physical and phenological. Chemical defense has been reported in buds, leaves, pollen, and bark (Laitinen *et al.* 2002, Rousi *et al.* 1996), and physical defense (Matsuki *et al.* 2004) and phenological strategies were deployed in leaves (Hagen *et al.* 2003). Birch defense is based on a system, and is not due to any single trait (Haukioja 2003).

### Incidence of the Proposed Defense Models in Birch Leaf Defense

There are species of 181 macro-lepidoptera and further insects that attack birches (Rousi *et al.* 2006), including *Lymantria dispar*, *Operophtera brumata* (Matsuki 2006), birch leaf-miner (*Fenusa fusilla*), and *Hamamelistes spinosus* aphids (Clement and Malinoski 2009). Although birch death due to insect attack is rare, insect defoliation often impairs the growth of birches (Rousi *et al.* 1996, 2006).

Defense of leaves, involving for example phenolic compounds, toughness, and trichomes, is important in preventing attack by herbivores (Matsuki 2006). Defensive strategies by birch leaves are more varied than by woody parts.

Some birch species are resistant to insect herbivores, but others are more susceptible (Koike *et al.* 2006a). Genetic variation in birch leaf defense has been found so as to protect against various insects. The mechanism of defense in birches appears to be species-specific (Rousi *et al.* 2006). In general, trees in which leaves have short lifespan have lesser defense capacity against insect herbivores (Koike *et al.* 2003, Matsuki and Koike 2006).

### Physical Defense

Physical defense of leaves is based on leaf toughness (Matsuki *et al.* 2004, Koike *et al.* 2006a), leaf mass per unit area (LMA) (Koike *et al.* 2003; Matsuki *et al.* 2006), trichomes (Rautio *et al.* 2002 and references therein; Traw and Dawson 2002) and some other traits. Leaf pubescence puts in place mechanical barriers, causing the leaf to become harder, tougher, and better equipped with defensive tools such as hair (trichome) or substances that are sticky or poisonous.

Most morphological defenses are in the category of constitutive resistance, but evidence also exists of inducible morphological defense (Rautio *et al.* 2002). Birch species have both glandular and non-glandular trichomes. Density of glandular trichomes decreases significantly as a result of simulated-defoliation (representing a reduction of photosynthetic capacity) whereas non-glandular trichomes tended to increase in number, on both the adaxial and abaxial side. The shifting may indicate that there is a trade-off between non-glandular and glandular trichome, or it was simply due to the different function of the two types of trichome (Rautio *et al.* 2002).

That study concluded that shifting between the two types of trichome can be explained by the different cost of producing the two types of trichomes. The cost is likely to be greater for glandular than non-glandular trichomes. When birch leaves faced intensive and repetitive damage of the leaves, which would presumably cause the loss of photosynthetic capacity, they adopted a less costly defense mechanism by producing non-glandular rather than glandular trichomes.

Matsuki *et al.* (2004) found that the physical defenses traits of leaves of three species of birch differ, i.e. are species-specific, suggesting that defense by birch leaves is controlled genetically. That study provided strong evidence against the growth-differentiation balance hypothesis (GDBH) (Herms and

Table 1. Defense methods used by birches

Plant organ	Defense type	Method of defense
Woody parts	- Chemical (top parts), constitutive	resin droplets contain triterpenoid (i.e. papyferic acid)
	- Chemical (basal parts), constitutive	Phenolic (i.e. platyphylloside and betulinic acid)
	- Freezing resistance	- Deep supercooling mechanism at xylem tissue - Extracellular freezing mechanism at phloem tissue
Bark of woody parts	- Chemical	Cathecin, flavonols, flavones, rhododendron, gallotannin, condensed tannin, Caffeoylquinic acid, cinnamic acid, platyphylloside, flavonoid aglicones
Leaf	- Physical	- Trichome (glandular and non-glandular) - Stomatal closure against O <sub>3</sub> loading
	- Phenology strategy	Autumn leaf color-change
	- Chemical (constitutive)	Phenolic compounds: condensed tannin, myricetin-3-gaactoside, quercetin-3-galactoside, catechin, chlorogenic acid. Triterpenoids: papyferic acid, pendulic acid
	- Chemical accumulation	condensed tannins, flavonoid (against UV-B radiation)
	- Chemical (induced)	H <sub>2</sub> O <sub>2</sub> against O <sub>3</sub> exposure

Summarized from Ruuhola and Yang (2006), Rousi *et al.* (2006), Laitinen (2004), Laitinen *et al.* (2004), Yamaji *et al.* (2003), Laitinen, M.-L. (2003), Ratio *et al.* (2002), Lavola (1998).

Mattson 1992), but favored the optimal defense hypothesis (ODH). This was also found by Riipi *et al.* (2002) in their study of birch leaf defense.

Matsuki *et al.* (2004) found that leaf toughness and trichome density in *B. maximowicziana* tended to be greater in late leaves than early leaves. In contrast, for *B. platyphylla* var. *japonica* (hereafter *B. platyphylla*) and *B. ermanii*, the density of trichomes was greater in early leaves than in late leaves. Stronger defense in early leaves of *B. platyphylla* and *B. ermanii* is contrary to predictions of the GDBH, because those birch species had a greater relative growth rate in the early stage of the growing season. This is probably due to the importance of early leaves for subsequent growth in both birch species (Clausen and Kozlowski 1965, Kozlowski and Clausen 1966, Koike 1995). In *B. maximowicziana*, however, there was no difference in growth rate between early and late stages, but late leaves are probably more valuable in *B. maximowicziana* than in *B. platyphylla* and *B. ermanii*, since the photosynthetic peaks later in the growing season, so that late leaves appear to be functionally important (Matsuki *et al.* 2004). Here, the ODH was in operation: defense was allocated preferentially to the more valuable organ.

### Chemical Defense

Young foliage is generally less well-defended against leaf-chewing herbivores, because of its high nutrient content and low condensed tannin concentration. Mature leaves that are poor in nitrogen and well defended by condensed tannin are unattractive to leaf-chewing insects (Lechowicz and St-Jacques 2000). Changes were found in the concentrations of phenols in birch leaves by Laitinen *et al.* (2002), during bud unfolding and leaf development.

Matsuki *et al.* (2004) found that the growth rate was higher at the early stage in *B. ermanii* and *B. platyphylla* than *B. maximowicziana*, but was higher at the late stage in *B. maximowicziana*. Chemical defense (total phenolic and condensed tannin content) tended to be higher for early leaves than for late leaves of *B.*

*ermanii* and *B. platyphylla*, but it was less in early leaves than in late leaves of *B. maximowicziana*. In *B. ermanii* and *B. platyphylla* the growth rate was higher, as well as defenses in the early stage. This observation is evidence against the GDBH, which predicts that plants with higher growth rates will have least defense.

The GDBH was also contrary to the results of Riipi *et al.* (2002), who found no trade-off between phenolic accumulation in leaves and the growth activity of birch leaves. Their study found that the European mountain birch (*B. pubescens*) was able to grow rapidly while simultaneously producing abundant secondary compounds. The correlation between growth rate and leaf phenolic content was positive in the summer and was not negative even in the spring when GDBH would predict the strongest trade-off. Accumulation of phenolics in birch leaves is therefore a regulated process, not a passive response to nutrient availability. This does not imply, however, that phenolics have evolved specifically for defensive roles; they might be produced for other functions as well.

Leaf phenolics and leaf nutrition traits are both involved in birch defense against insects. Leaf defense in birch is probably due to various chemical and physical mechanisms that operate together, and is not the work of any one group of compounds (Haukioja 2003).

Some evidence supports the carbon nutrient balance hypothesis (CNBH). Keinänen *et al.* (1999) stated that the leaves of fertilized saplings contain lower levels of condensed tannins than did controls, consistent with the CNBH, although their study also found that the accumulation of phenolics was strongly coordinated, possibly by enzyme activities.

### Role of Woody Parts of Birch in Defense

Hares, moose, voles (Rousi *et al.* 1996, Rousi 2000, Rousi *et al.* 2006, Laitinen 2004) and Sika-deer (Nagai *et al.* 2000) are all mammals that browse on young birch stems. Larvae of the bronze birch borer beetles (*Agrilus anxius*) are known to attack mature birch stems (Clement and Malinoski 2009).

Table 2. Main trends in phenolic concentration during bud unfolding and leaf development

Group	Main trend
1. Hydrolysable tannins	↓
2. Flavanoid aglycones	↓
3. Catechin derivates	↓
4. DHPPG (3,4'-dihydroxypropiophenone-3- <i>b</i> -D-glucoside)	↑
5. Phenolic acid	↑
6. Flavonol glycoside	↑
7. Low molecular weight phenolic	--

Note: ↑ = increasing concentration;  
↓ = decreasing concentration;  
-- = no clear trend

Cited from Laitinen *et al.* (2002) with permission.

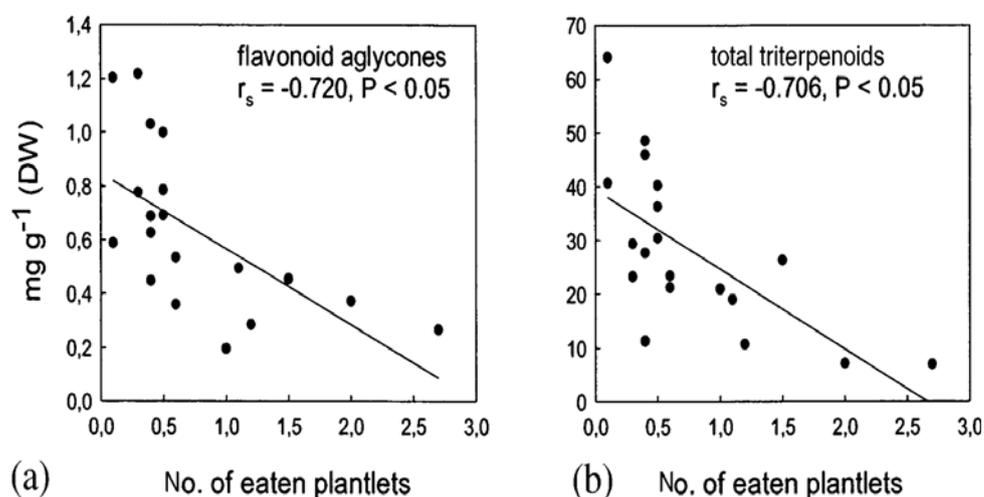


Fig. 1. Relation between palatability and chemicals in birch bark; (a) for flavonoid aglycones, and (b) for total triterpenoid (Cited from Laitinen, M.-L. *et al.* 2004, with permission).

The woody parts of birches protect themselves chemically against browsing by herbivores such as hares (*Lepus timidus*) (Rousi *et al.* 1996). Against the bronze birch borer beetle, human assistance by pruning or the use of pesticide on the attacked part is effective (Clement and Malinoski 2009).

Variations are found in the resistance of woody parts to mammal herbivores. The preference of the mammals stated for birch species is due to the palatability of birch, which in turn is determined by the chemical contents of its woody parts (Rousi 2000). Vertical differences exist in defense by birch stems. Basal parts contain phenolics as the main defensive compounds, which deter hares and voles (Palo 1985, Risenhower *et al.* 1985), whereas defense in the top shoots is based probably on terpenoids contained in the resin droplets that deter moose (Tahvanainen *et al.* 1991).

The phenolic compound known as platyphylloside can inhibit digestive processes of mammals, both *in vitro* and *in vivo* (Palo 1985, Sunnerheim 2006). Tahvanainen *et al.* (1991) nevertheless believe that, although a significant positive correlation prevails between phenolics and the palatability of birch seedlings, these compounds are probably not the main factor determining preferences among seedlings by hares, since the variation of phenolic content between tested seedlings is small.

Keinanen *et al.* (1999) found that different branches of the biosynthetic pathway of phenolic compounds may compete with each other for substrates. The resulting internal metabolic trade-off may explain the differential accumulation of the compounds; this is supported by the fact that, in fertilized saplings, the concentration of condensed tannins correlates negatively with the amount of triterpenoid resin droplets. Trade-off between the biosynthetic routes to terpenoids and flavanoid derivatives (such as condensed tannins) may therefore be due to a linkage via malonyl-CoA.

The bark of birch also has an important role in herbivory resistance (Laitinen *et al.* 2004). Total

triterpenoid and total flavonoid aglycones showed a significant negative correlation with hare feeding. This study also found that variations in triterpenoid content were high, whereas phenolics exhibited rather low variation within the genotype tested. Tahvanainen *et al.* (1991) similarly reported large variations in terpenoids but smaller variations in phenolics. It follows that the accumulation of triterpenoid is more sensitive to environment than for phenols. Consequently, a genetic basis for bark chemistry and resistance in birches is likely strong, although the environment may alter the amount of defensive compounds, especially terpenoids. The inter-relation of genotype and environment in the defensive chemistry of birch bark is still unclear (Fig. 1).

Laitinen *et al.* (2002) tested the CNBH by growing birches in different soil types. Their result partly supported the CNBH, since trees grown in nutritious soil (optimal condition) had fewer resin droplets at the shoot than those grown in peaty soil (low nutrient). There was no significant interaction, however, between genotype and habitat in the production of resin and growth/palatability, indicating that different tree genotypes can have distinct responses to environmental variation (e.g. Matsuki 2003). There appears to be a strong genetic basis for resistance, since the correlation between height and palatability of birches was negative in 1-year-old seedlings but positive in the 8-year-old saplings. This suggests that first-year seedlings attain optimal growth as well as high defensive chemical given high nutrient supply, with no trade-off between growth and resistance. Thus, the responses of all birch clones did not conform to the predictions of the CNBH.

In general, the woody parts of birch have a constitutive defense type, by having secondary metabolites that impede the predator, although the production of some secondary metabolites is also induced when this plant is under stress due to abiotic and biotic pressures (Almeida-Cortez *et al.* 2004, Eranen 2009, Laitinen 2003, Riipi *et al.* 2002).

### Influence of Abiotic Factors on Birch Defense

Plant metabolism, growth and development, as well as the level of defense, can be altered substantially by environmental conditions, including UV-light, soil nutrient levels, elevated CO<sub>2</sub>, ozone levels, defoliation, extraordinary temperatures (Bryant *et al.* 1987, Lavola and Julkunen-Titto 1994, Lavola *et al.* 1994, Rousi *et al.* 1996, Lavola 1998), plant age (Bryant and Julkunen-Titto 1995, Laitinen 2003), type of plant tissue (Tahvanainen *et al.* 1991), and season (Matsuki 2006).

Lavola and Julkunen-Titto (1994) suggested that production of phytochemicals in birch is very sensitive to fertilization (Bryant *et al.* 1987) and to CO<sub>2</sub> enrichment (Koike *et al.* 2006c); this provides some support for the CNBH, such that plants allocate carbon for defense when it is in excess. Minor soluble sugars (such as fructose and glucose) decreased with an increase in fertilizer applied, while the main sugar, sucrose, was unaffected. CO<sub>2</sub> enhancement (Lavola and Julkunen-Titto 1994) and ozone (Lavola *et al.* 1994) had greater effects on soluble sugar in leaves than in stem.

There are large differences in responses to ozone enrichment according to birch genotype. Some genotypes responded by changing the allocation of carbon toward the roots, by stomatal closure (thereby reducing ozone uptake), and by investment in low-cost foliar antioxidants (such as chlorogenic acid) to avoid and better tolerate ozone stresses. Other genotypes exhibited defense by increasing the root/shoot ratio, and relied on inducible high-cost antioxidants (such as flavonoid aglycones); additionally, they increased the production of leaves in number so as to compensate for the decline in the leaf level net photosynthetic rate due to the presence of ozone.

The best ozone tolerance is found among genotypes that have a high constitutive amount of total phenolics, high investment in low-cost antioxidants (such as chlorogenic acid) and lower stomatal conductance under ozone stress (Yamaji *et al.* 2003). Ozone delays bud bursting, induces visible foliar injuries, and damages the ultrastructure in chloroplasts (Rousi *et al.* 2006). It also impairs net photosynthesis (Oksanen *et al.* 2005), resulting in long-term growth loss (Rousi *et al.* 2006).

According to the CNBH, the increase of CO<sub>2</sub> under normal conditions of nutrient availability should increase plant growth, photosynthesis, and carbohydrate concentrations. However, Lavola and Julkunen-Titto (1994) found that the production of mobile secondary metabolites (such as phenolic glycoside) did not respond consistently with CNBH predictions, or if so then the response was small. Immobile phenolic metabolites (i.e. proanthocyanidin and flavanoid) were likely to respond to fertilizers and had altered carbon balance, as predicted by the CNBH. In general, however, little evidence was found for trade-off, either between responses in resistance to different predatory factors or between growth rate and defensive response of birches, since great variations exist in the plant defense response (Rousi *et al.* 2006).

Although their effect was not strong, shading and

fertilization have different effects in birch defense against hares and voles. The resistance of the top parts of the seedlings to hares increased with increasing application of fertilizer, whereas shading decreased it. In contrast, more fertilizer reduced the resistance to voles of the basal part of the seedling, whereas shading tended to increase it (Rousi *et al.* 1993, Mutikainen *et al.* 2000). In this case, fertilization appears to have increased the amount of resin droplets, rendering the shoots of the seedlings more resistant to hares. Also, phenolics decreased as main defensive compounds in the basal part as a result of nitrogen fertilization, making this part become more vulnerable to voles (Rousi 2000). Several studies have found that nitrogen fertilization may actually decrease the phenolic content of plant tissues (Rousi *et al.* 1993) (Fig. 2).

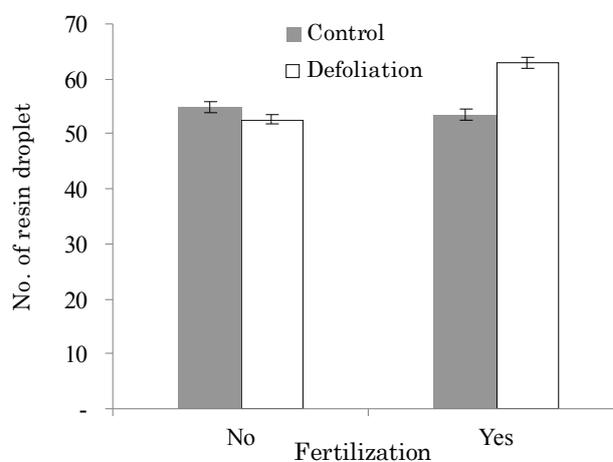


Fig. 2. Mean number of resin droplets at the tip of non-fertilized and fertilized *B. pendula* saplings (Cited from Mutikainen *et al.* 2000, with permission).

According to the CNBH (Bryant *et al.* 1983), the level of chemical defense should be flexible in phenotypic traits that are strongly influenced by environmental conditions. However, Tahvanainen *et al.* (1991) found great variability in the content of secondary metabolites among experimental birch seedlings grown in homogenous environmental conditions in a greenhouse, and concluded that this variability is controlled genetically. They found no trade-off between the growth of birch and its chemical defense. Rousi (2000) similarly stated that there is no clear evidence for support of the CNBH in birch species. In the white birch, rapid growth and high resistance capacity are coincided.

Birches, which live in the cool northern hemisphere, enact freeze resistance during the winter season. Lechowicz and St-Jacques (2000) found that trees which are more vulnerable to freeze-damage are also more prone to be attacked by insect herbivores. The more intensive insect attack was attributed to the greater relative abundance of young foliage on the trees that were damaged. This study found that freeze-damaged trees produce more young foliage later in the season than undamaged trees, as compensation

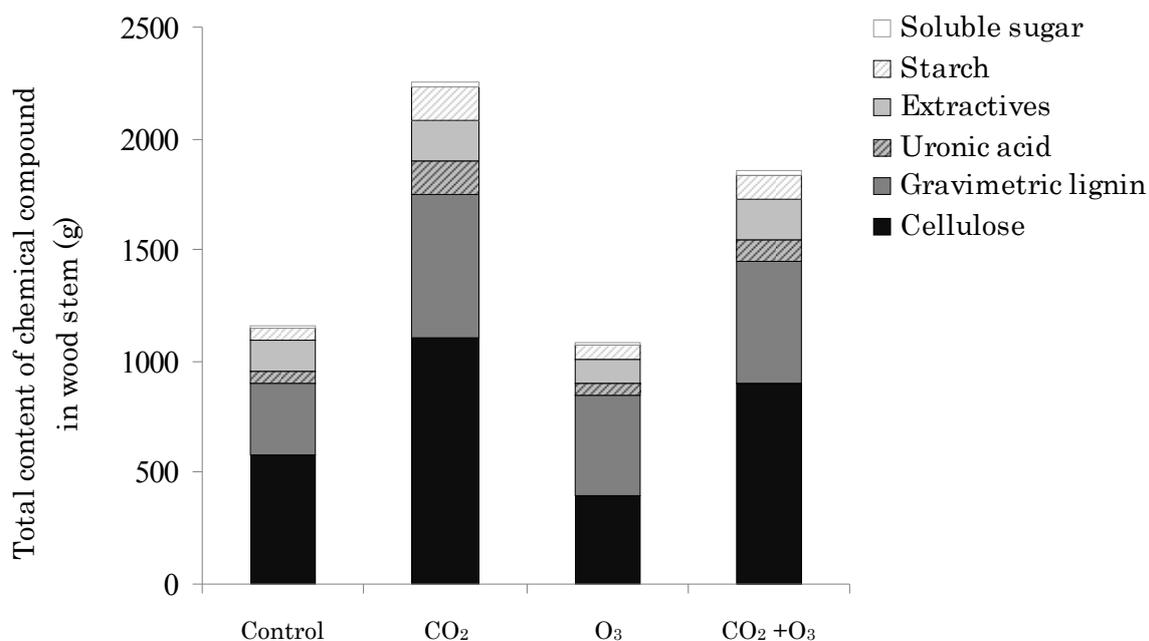


Fig. 3. Effects of 5 years (1998-2002) of exposure to elevated CO<sub>2</sub> and O<sub>3</sub> alone, or in combination, on dry mass and absolute content of chemical compounds (g stem<sup>-1</sup>) in paper birch wood stem (Cited with modification from Kostianinen *et al.* 2008).

for early-leaves killed or developmentally stunted by freezing events.

In general, the terpenoids were strongly influenced by the environment, and these effects were genotype-specific. Ontogeny also had very a strong effect on terpenoids; the content in four-year-old birch plantlets was 100 times higher than in 20-year-old trees. For some phenolic glycosides, such as platyphylloside, the growth environment and ontogeny have only small effects, although variation between genotypes is large (Laitinen *et al.* 2005).

The concentration of phenols in birch shows seasonal trends between bud unfolding and leaf development. Young foliage contains a higher concentration of the hydrolysable tannin, gallotannin. Its concentration declines during bud unfolding and leaf development, whereas the concentrations of phenolic acid, flavonol glycosides and condensed tannins tend to increase. These differences are due to the biosynthetic origin of these compounds. Biosynthesis of gallotannin can proceed without direct competition with protein synthesis, which is essential during the initial growth. Synthesis of phenolics in mature leaves occurs at the time of change from exponential growth to the stationary phase, where there is less competition with protein synthesis. The increase in flavonol glycoside concentration during later leaf development may therefore be due to the transitional time of growth (from exponential to the stationary phase) (Laitinen 2003) and to UV-light radiation (Lavola 1998).

Elevated CO<sub>2</sub> and temperature increase the growth of young birches (Pettersson *et al.* 1993). Elevated CO<sub>2</sub> also increases the number of lateral branches of the seedlings. This response appears to be genotype-specific. Increased UV-B radiation, on the other hand, has only a small effect on the growth and morphology

of young birches (Rousi *et al.* 2006) (Fig. 3).

Biotic and abiotic resistance of trees may be strongly correlated with adaptability, chemical profile, phenology, flowering, growth, and competitive interactions. Interactions of these traits will determine the fitness of birch defense genotypes (Rousi 2000).

In dealing with biotic and abiotic stresses, birches have several modes of defense. This defense exhibits great variations, within individual trees, within species, between seasons, and in differing environmental conditions. Birches generally have at least three types of defense, including physical and chemical (whether constitutive or induced), and also a phenological strategy.

Birches undergo acclimation and adaptation due to defense against biotic and abiotic factors; mountain birch (*Betula pubescens* subsp. *czerepanovii*), for example, has evolved resistance to heavy metals. This adapted resistance to heavy metals has given rise to co-resistance against biotic stress and mountain birches are consumed less by insect herbivores (Eranen 2009).

Chemical defense usually imposes an energy cost such that resistance to herbivores is metabolically expensive for the plant. In some cases there was a positive relationship between growth and resistance, consistent with the CNBH or the GDBH, but in others there was no relation between them at all (Rousi *et al.* 1993).

There is no clear evidence of a trade-off between birch defense and growth, since birch defense is believed to be controlled genetically (i.e. Rousi *et al.* 1993; Mutikainen *et al.* 2002, Tahvanainen *et al.* 1991, Laitinen *et al.* 2002, Lavola and Julkunen-Tiitto 1994, etc). Many studies suggest that there is no trade-off involved in birch defense, and that plants do not noticeably shift their energy to defense so that growth is

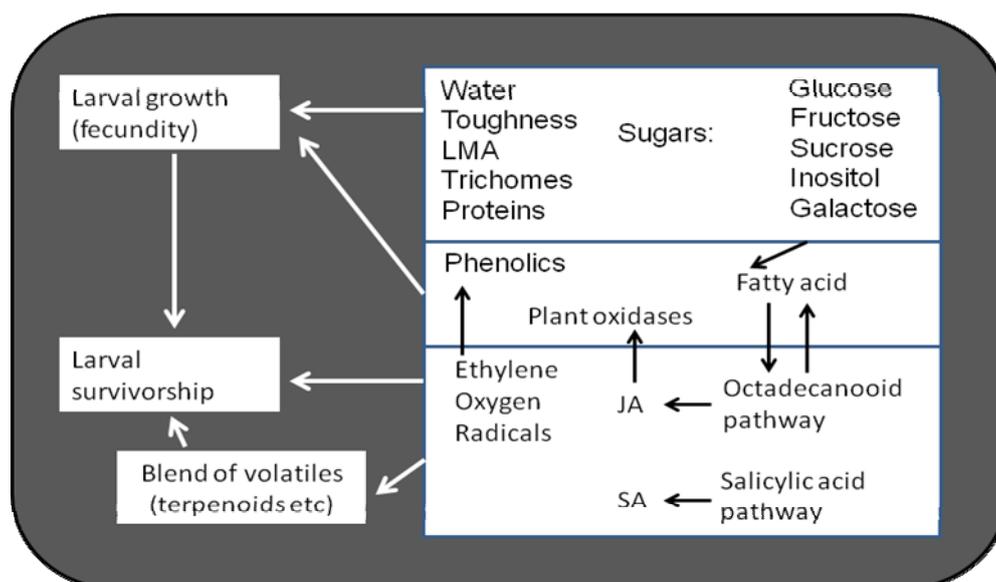


Fig. 4. Mechanisms involved in birch defense (Modified from Haukioja 2003).

less disturbed by the defense energy allocation; but attack by herbivores can still cause serious problems in productivity of birch plants. Trunk browsing and leaf defoliation obviously decrease the plant biomass. When insect attack is severe, leaf defoliation can reduce the photosynthetic rate, in turn impairing plant productivity. Thus, the effort of reducing damage by herbivory more relies on selecting resistant genotypes (Rousi *et al.* 2006).

The great variations in birch defense are a consequence of the several modes of defense available, depending on the type of predator, and on biotic and/or abiotic stresses. This variation is genetically controlled, so that evidence supporting the CNBH in birch defense is rarely found. Defenses of the birch arose through adaptation and evolution and developed over long periods of time. Well-known defense models such as the GDBH, the CNBH, or the ODH are likely inadequate, although further research is needed to settle the question. This would consider ontogeny, and use labeled radioactive compounds to track carbon/compound allocation (Bryant and Julkunen-Tiitto 1995) or other sophisticated tools.

We believe that defense systems in birches do not always depend on growth rate or the availability of resources, and can be understood fully only in an evolutionary context (Stamp 2003) (Fig. 4).

### Conclusion

Birch defense is highly complex; since the testing of plant defense hypotheses is based on the measurement of crude indices (such defense chemical compound, i.e. triterpeneoid or phenolic) that undergo have large variation. We assert that birch defense functions act in parallel via the simultaneous deployment of chemical and physical mechanisms as proposed by Haukioja (2003).

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