

Gilles Houle · Geneviève Simard

Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* ssp. *planifolia* to simulated herbivory

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Abstract Plant responses to herbivory include tolerance (i.e. compensatory growth) and defense. Several factors influence the tolerance of a plant following herbivory, including plant genetic identity, site nutrient availability, and previous and/or concurrent herbivory. We studied the effects of these factors on the compensatory response of *Salix planifolia* ssp. *planifolia*, a shrub species common in the boreal and subarctic regions of North America. We cloned several genets of *S. planifolia* and submitted them to simulated root and/or leaf herbivory while varying the nutrient availability. Simulated leaf herbivory was more detrimental to the plant than simulated root herbivory, reducing both above- and below-ground tissue production. Leaf demography was unaffected by either simulated herbivory treatment. There was some compensatory growth following simulated leaf and root herbivory, but only the root compartment responded to increased nutrient availability. Simulated leaf herbivory increased leaf transpiration and reduced stomatal resistance, suggesting increased carbon fixation. The unexpected finding of the experiment was the absence of interactions among factors (genotype, nutrient availability and type of tissue damage) on the compensatory response of *S. planifolia*. These factors thus have additive effects on the species' compensatory ability.

Key words Nutrient addition · Plant compensation · Plant tolerance · Relative growth rate · Stomatal resistance

Introduction

By selecting specific genotypes or populations of plants, herbivores have the potential to significantly influence the genetic composition of populations or the specific composition of communities (McNaughton 1983; Herms and Mattson 1992). Yet, the ability of plants to respond to herbivory may vary considerably both intra- and inter-

specifically (Maschinski and Whitham 1989; Senn and Haukioja 1994). Evidently, plant genetic identity influences these two aspects of herbivory, i.e. plant susceptibility and response to herbivory (Crawley 1983; Marquis 1984; Rosenthal and Kotanen 1994).

Plant response to herbivory may be quite different if herbivores attack below-ground structures from if they use above-ground tissues only (Detling et al. 1980; Prins et al. 1992). In fact, herbivory cumulated both at the above- and the below-ground levels may severely affect a plant, often in complex (non-additive) ways (Reichman and Smith 1991). Plants growing in high-stress habitats may not be able to restore the biomass lost to herbivores as effectively as plants growing in low stress sites (Belsky 1986; Chapin and McNaughton 1989; Maschinski and Whitham 1989; Müller-Schärer 1991; Steinger and Müller-Schärer 1992; Hjäältén et al. 1993; but see Hilbert et al. 1981; Hicks and Reader 1995). In addition, nutrient- or water-stressed plants may be more attractive to herbivores than non-stressed ones (White 1984; Mattson and Haack 1987; but see Price 1991).

Many studies have considered the ifs and hows of plant compensation (tolerance) to herbivory, compensation being defined as the ability of plants to make up for tissues lost to herbivores. As defined by Belsky (1986), final biomass plus biomass of lost tissues in predated plants must equal final biomass of intact plants for full compensation to have occurred; however, tissues lost to herbivores make no contribution to plant fitness (Gedge and Maun 1992; Vail 1992). Compensation (from a plant perspective) may be better defined in physiological terms, increased relative growth rate or net photosynthesis in predated plants being considered the compensatory response (Heichel and Turner 1983; Rosenthal and Kotanen 1994). For compensation in the fitness sense of the term to occur, clearly physiological compensation must be present; yet, physiological compensation may occur but not to the point of bringing the fitness of a predated plant to the level of that of an intact plant.

In the present study, we cloned genets of a woody species, *Salix planifolia* Pursh ssp. *planifolia* and sub-

G. Houle (✉) · G. Simard
Centre d'études nordiques and Département de biologie,
Université Laval, Sainte-Foy, Québec, Canada G1K 7P4

mitted the ramets produced to different levels of nutrient availability in combination to simulated herbivory at the root and/or leaf level. Although several studies have considered the defense response of willows to herbivory (Palo 1984; Danell et al. 1985; Tahvanainen et al. 1985; Julkunen-Tiitto 1986; Danell et al. 1987; Elmqvist et al. 1988; Rank 1992), few have reported the significance of tolerance, i.e. compensation (e.g. Wolff 1978; Roininen and Tahvanainen 1991; DeClerck-Floate and Price 1994). We hypothesized that tolerance response to simulated herbivory in *S. planifolia* would depend upon complex interactions between genotype, type of tissue damage, and nutrient availability.

Materials and methods

The species

Salix planifolia ssp. *planifolia* is a North American shrub species mostly of boreal and subarctic distribution. It grows on river and stream banks, around fens and bogs, more rarely on screes and in cracks on rock outcrops. In northern Québec, it is one of the most common willow species where it often forms extensive monospecific stands in riparian zones. The presence of secondary metabolites (e.g. phenolic glycosides) has been verified in the leaves and bark of several willow species, including species taxonomically very close to *S. planifolia* (e.g. Palo 1984; Tahvanainen et al. 1985; Julkunen-Tiitto 1986). Yet insect damage to the leaves of *S. planifolia* can be severe (G. Houle, personal observations).

Study site

The study was conducted in Whapmagoostui-Kuujuaraapik (Great Whale), a small village on the east coast of Hudson Bay, in northern Québec. Mean annual temperature at the Great Whale meteorological station (55°17'N, 77°46'W, 18 m asl) is -4.3°C and annual precipitation averages 650 mm with 40% falling as snow (Atmospheric Environment Service 1981). The frost-free period in the area lasts on average 77 days (Atmospheric Environment Service 1982).

Experimental design

In early June 1993, 30 cuttings 0.5–1 cm in diameter were collected from each of 20 *S. planifolia* shrubs from a population along the Great Whale River, in Whapmagoostui-Kuujuaraapik. Cuttings were uniformly cut to a length of 20 cm and two incisions were made at their base before they were put to soak for 24 h in water. Immediately before planting, the base of the cuttings was dipped for c. 5 s in a 1000 ppm alcoholic solution of indol-3-butyric acid (IBA). Cuttings were planted in containers of 45 cavities (110 cm³) in a sand – peat moss mixture (3:1). The experiment was carried out in a greenhouse in Whapmagoostui-Kuujuaraapik; photoperiod during the experiment was maintained at 16 h, minimum temperature at 15°C, and maximum temperature at 25°C. After 4 weeks, the cuttings were taken out of their cavities and 24 rooted cuttings per clone (i.e. *Salix* shrub) were randomly selected for simulated herbivory experiment (only 13 clones had sufficient rooted cuttings, i.e. 24, for the subsequent experiment).

Then, cuttings from each clone received one of the following treatments (randomly assigned within clone): simulated root herbivory (50% of the roots, i.e. every other root, cut to 50% of their length); simulated leaf herbivory (50% of the leaves, i.e. every other leaf, cut to 50% of their length); simulated root and leaf herbivory (combination of the above treatments); and no simulated herbivory. The cuttings were then transplanted in containers of 25

cavities (200 cm³) in a substrate mixture as above. Superimposed on the herbivory treatments, was a nutrient addition treatment with 0, 0.5 and 1 dose of the recommended concentration of a complete commercial fertilizer (20–20–20), at a rate of 5 ml per cutting. Nutrient addition treatments were applied twice during the experiment, at the beginning (3 July 1993) and mid way through (24 July 1993). Treatment combinations were randomly attributed to cuttings of a given clone, with two replicates per treatment combination (for a total of 24 cuttings per clone). When the simulated herbivory treatments were applied, the number of leaves and the number of roots produced per cutting were determined and the leaf and/or root material removed was kept, oven-dried at 75°C for 36 h and then weighed. Plants were watered every day for the 5 weeks of the experiment.

From 3 July 1993 to 7 August 1993, we made the following measurements weekly: number of leaves, and leaf transpiration and stomatal resistance (with a LI-1600 steady state porometer from Li-Cor). At the end of the experiment, leaf, root and cutting mass was determined for each plant, after drying for 36 h at 75°C. New shoot and root relative growth rates (RGR) were calculated assuming that 25% of the leaf and/or root material was removed by the simulated herbivory treatments to calculate initial (before simulated herbivory) mean mass of leaf or root tissues. We also estimated that leaves made up approximately 95% of the new shoot biomass, giving the following estimates (see results below, for mass of tissues removed following simulated herbivory):

1. Initial leaf mass: 60 mg×4=240 mg
2. Initial new shoot mass: 240 mg/0.95=253 mg
3. Initial root mass: 12 mg×4=48 mg
4. RGR for new shoots (linear model):
control: [(final new shoot biomass – 253 mg)/253 mg]/35 days
simulated leaf herbivory:
[(final new shoot biomass – 193 mg)/193 mg]/35 days
5. RGR for roots (linear model):
control: [(final root biomass – 48 mg)/48 mg]/35 days
simulated root herbivory:
[(final root biomass – 36 mg)/36 mg]/35 days

Four-factor (clone, nutrient addition, leaf and root herbivory) analyses of variance (mixed model) were done for the different variables (for the root:shoot ratio, the ANOVA was done on arcsine-transformed data). For the leaf transpiration and stomatal resistance data, one ANOVA was done for each of the five sampling dates and, consequently, we adjusted the *P*-value at 0.05/5, i.e. *P*' = 0.01 (Bonferroni correction).

Results

Leaf and root number at the beginning of the simulated herbivory experiment did not differ significantly between treatments (Table 1; overall mean ±1 SEM was 21.4±0.4 leaves and 10.5±0.3 roots). Simulated leaf and root herbivory removed a significant amount of tissue: 60±4 mg and 12±1 mg for the simulated leaf and root herbivory treatments, respectively (Table 1).

Root biomass was reduced by both the root and the leaf herbivory treatments (13% and 11%, respectively), but it was increased (11% and 19% for nutrient addition levels 0.5 and 1, respectively) by nutrient addition (Table 1 and Fig. 1). Final new shoot biomass varied significantly among clones, and it was decreased (18%) by leaf herbivory, although root herbivory or nutrient addition had no significant effects on these above-ground tissues (Table 1 and Fig. 1). Final cutting mass was unaffected by either one of the three treatments (leaf and root herbivory, and nutrient addition), but it varied among clones

Table 1 Significance level (*P*) for the different factors from the four-factorial analyses of variance performed on the variables considered. (*C* clone effect, *L* leaf-removal effect, *R* root-removal effect, *F* fertilization effect). For leaf transpiration and stomatal resistance, only effects significant at least at $P < 0.01$ (i.e. $P < 0.05/5$, Bonferroni correction) are indicated. There were no significant interactions among factors except a *L*×*R* interaction ($P < 0.05$) for green shoot relative growth rate, and a *C*×*L*×*R* and *C*×*L*×*F* interaction ($P < 0.01$ and $P < 0.005$, respectively) for leaf transpiration on 24 July 1993

Variables	Factors			
	C	L	R	F
Initial leaf number	–	–	–	–
Initial root number	–	–	–	–
Biomass removed				
Roots	–	–	*4	–
Leaves	–	*4	–	–
Final biomass				
Roots	–	*3	*3	*3
Cutting	*1	–	–	–
Green shoots	*1	*4	–	–
Root:shoot ratio	–	–	–	–
Relative growth rate				
Roots	–	*3	*3	*3
Green shoots	*1	*1	–	–
Leaf demography				
New leaves produced	–	–	–	–
Leaves having died	–	–	–	–
Final leaf number	–	–	–	–
Transpiration				
07–10–93	*3	*4	*2	–
07–17–93	*3	*3	–	–
07–24–93	–	*4	–	–
07–31–93	–	–	–	–
08–07–93	–	–	–	–
Stomatal resistance				
07–10–93	–	–	–	–
07–17–93	–	–	–	–
07–24–93	–	*3	–	–
07–31–93	–	*2	–	–
08–07–93	–	–	–	–

– $P > 0.05$; *1 $P < 0.05$; *2 $P < 0.01$; *3 $P < 0.005$; *4 $P < 0.001$

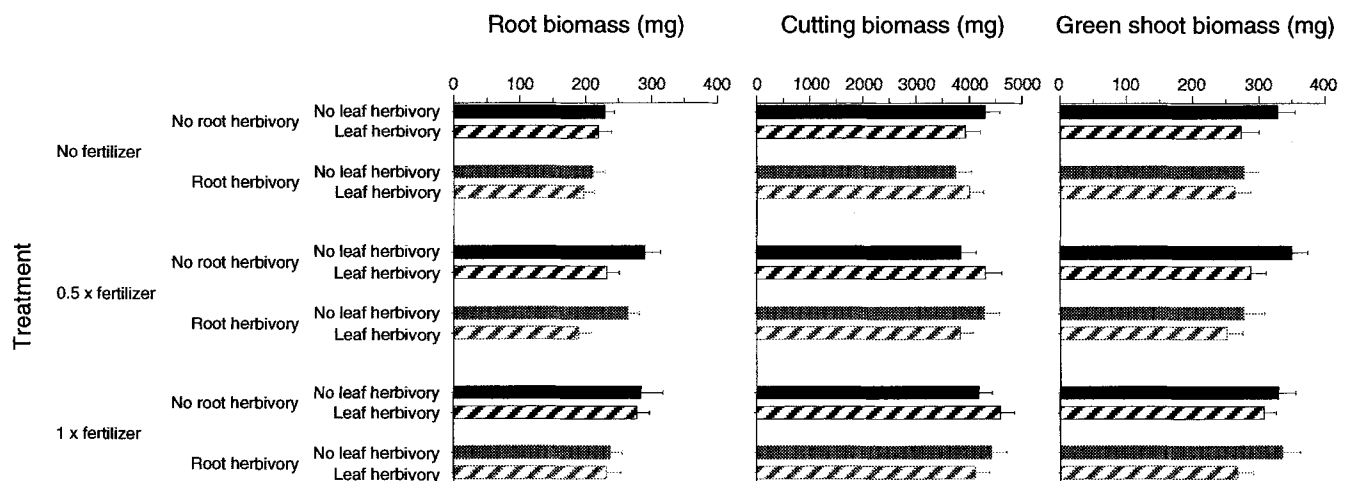
(Table 1 and Fig. 1). Root:shoot ratio, at the end of the experiment, was not significantly affected by clonal origin, root or shoot herbivory nor by nutrient addition (Table 1): overall mean ± 1 SEM was 0.808 ± 0.015 .

Above-ground relative growth rate (RGR) varied significantly among clones and was increased (44%) by leaf herbivory, but it was unaffected by root herbivory or nutrient addition (Table 1 and Fig. 2). Below-ground RGR was reduced (14%) by leaf herbivory, but it was increased by root herbivory (19%) and nutrient addition (17% and 24% for nutrient addition levels 0.5 and 1, respectively); there were no significant differences in root RGR among clones (Table 1 and Fig. 2).

Leaf demography (birth and death) was not affected by the treatments or by clonal identity (overall mean ± 1 SEM: 1.2 ± 0.1 new leaves and 7.5 ± 0.3 dead leaves per cutting, during the study period); the result was that leaf number at the end of the experiment did not differ significantly between treatments or among clones (Table 1; overall mean ± 1 SEM was 15.4 ± 0.3 leaves per cutting). Leaf transpiration and stomatal resistance most often differed between simulated leaf herbivory treatments, but not between simulated root herbivory treatments (except for one sampling date): transpiration was higher and stomatal resistance was lower for leaves of plants from the simulated leaf herbivory treatment (Table 1 and Fig. 3). Clonal identity affected significantly leaf transpiration immediately after the herbivory and nutrient addition treatments (first two weeks), but not thereafter (Table 1).

The most unexpected result of the experiment was the lack of significant interactions among factors in the analyses of variance. Of 253 possible two-, three- and four-way interactions, only three were significant (Table 1). This emphasizes the strictly additive effects of our treatments on the compensatory response of *Salix planifolia*.

Fig. 1 Biomass (mg) of green shoots, woody cuttings and roots of *Salix planifolia* according to treatment, 5 weeks after the beginning of the experiment



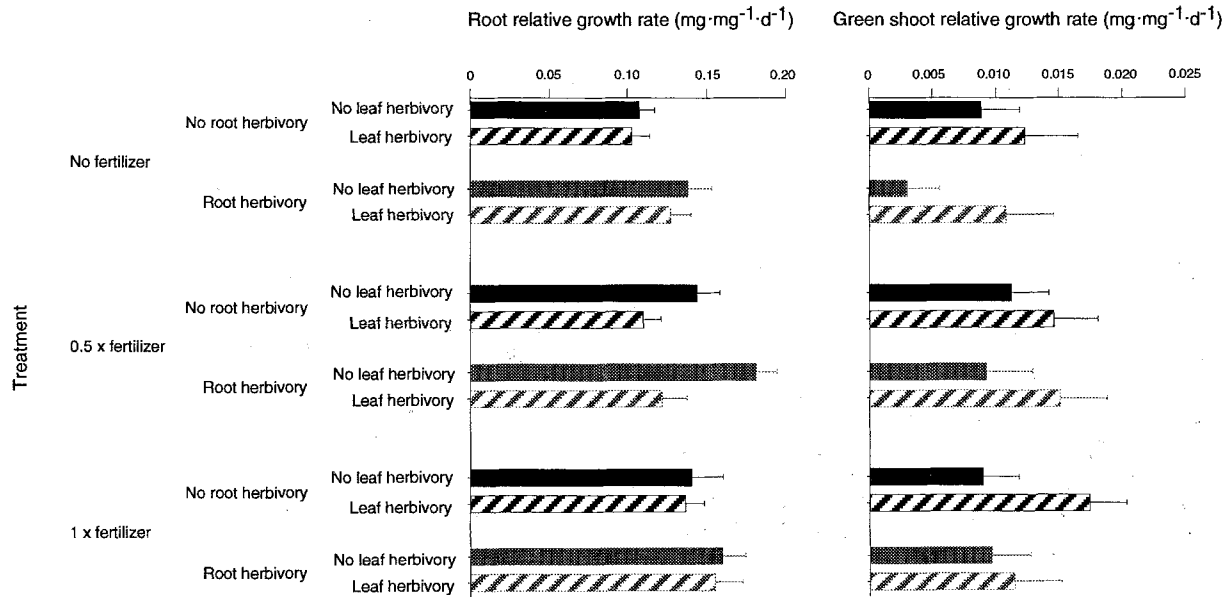
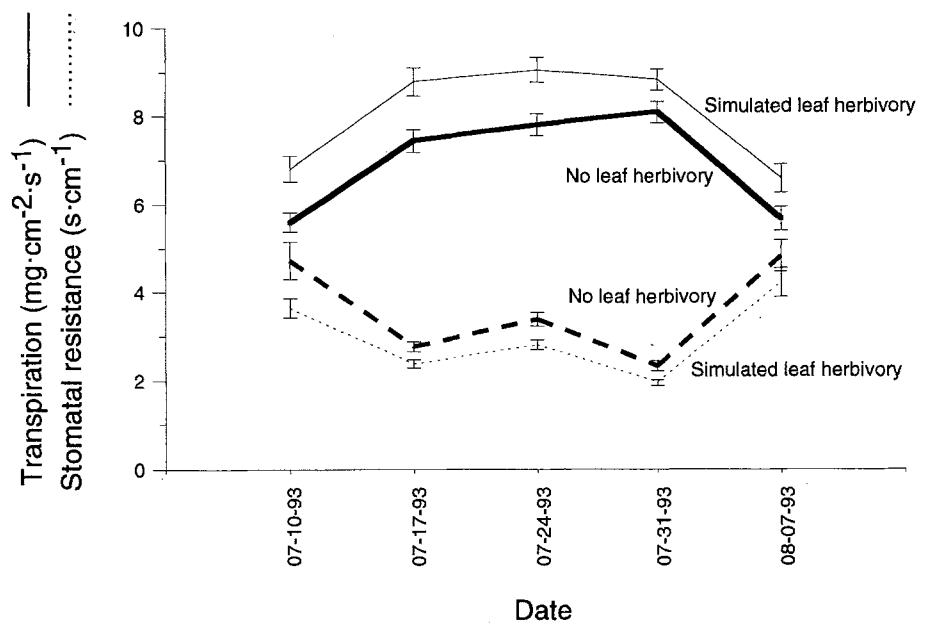


Fig. 2 Green shoot and root relative growth rate (mg·mg⁻¹·d⁻¹) of *S. planifolia* according to treatment, over the 5 weeks of the experiment

Fig. 3 Leaf transpiration (solid line) and stomatal resistance (dotted line) according to leaf herbivory treatment (no herbivory heavy line, simulated herbivory fine line), over the 5 weeks of the experiment



Discussion

Leaf herbivory is much more detrimental to *S. planifolia* than root herbivory, reducing both green shoot and root biomass, and root RGR (see also Ryle and Powell 1975; Richards 1984; Masters and Brown 1992; Oosterheld 1992; but see Detling et al. 1980; McNaughton and Chapin 1985; Reichman and Smith 1991; Prins et al. 1992). Leaf demography (birth, death, and longevity) is not altered by the simulated herbivory treatments, but leaf physiology is, as lower stomatal resistance for the simulated leaf herbivory plants suggests higher photosynthetic rate (Caldwell et al. 1981; Heichel and Turner 1983; Nowak and Caldwell 1984; Wallace et al. 1984; Hik and

Jefferies 1990; Bowman and Conant 1994). Presumed higher photosynthetic activity and concurrent higher green shoot RGR indicate some degree of compensation as a result of leaf herbivory: in fact, in the simulated leaf herbivory treatment, new shoot biomass at the end of the experiment was c. 82% of that of the control (from an initial value of 75% of the control immediately after simulated herbivory).

Higher root RGR as a result of simulated root herbivory is also a compensatory response, but one that does not appear to be associated with increased photosynthetic activity and that is not manifested at the expense of above-ground growth: final root biomass in the simulated root herbivory treatment represented c. 88% of that of

the control (from an initial value of 75% of the control immediately after simulated herbivory). Higher new shoot RGR appears to depend upon stored reserves (e.g. in the woody cutting) because it is unaffected by nutrient addition, while root RGR depends at least in part upon nutrient availability in the soil (but see Trumble et al. 1993).

Above-ground growth thus seems to be favored at the expense of below-ground growth following simulated leaf herbivory. However, the converse is not true: following simulated root herbivory, there is no trade-off between below- and above-ground growth. There is an apparent asymmetry in the dependence of the two biomass components (above- and below-ground) in the face of tissue destruction: the premium appears to be on leaf area. Yet, the root-shoot ratio is restored to 'normal' value after simulated leaf or root herbivory (see Richards 1984); allometric relationships are thus maintained.

Willows appear to be able not only to chemically defend themselves against herbivory (e.g. Palo 1984; Julkunen-Tiitto 1986) but can apparently also tolerate (i.e. compensate for) tissue loss (e.g. Wolff 1978). Increased photosynthetic rate following herbivory, a likely compensatory mechanism associated with lower stomatal resistance and higher transpiration, may be possible because of the most typical habitat of willows, that is water-saturated soil. Yet, because the species studied also occur on more xeric sites (e.g. on rock outcrops), an adjustment in the photosynthetic rate may there be restrained by higher stomatal resistance induced by leaf herbivory to reduce leaf transpiration rate. We propose that under such conditions tolerance may be a less significant response to herbivory than resistance: not only the intensity of, but also the type of response to herbivory may thus be resource-dependent.

We initially proposed that compensation would depend upon complex interactions between genetic identity, type of tissue damage, and nutrient availability. The lack of interactions between these factors in the analyses of variance is thus unexpected (see Swank and Oechel 1991; Honkanen et al. 1994; Senn and Haukioja 1994; Hakulinen et al. 1995; but Strauss 1991). This result indicates that the treatment effects are strictly additive for all the clones studied. In consequence, although clones may differ in their inherent compensatory response, nutrient availability and type of tissue damage influence compensation similarly among clones.

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