

Ontogenetic switches from plant resistance to tolerance: minimizing costs with age?

Karina Boege,* Rodolfo Dirzo,
David Siemens and Paul Brown

Department of Biological, Sciences,
Stanford University, Stanford, CA

Ecology Letters (2007) 10: 177–187

My Interest

I have been interested in “**Size- and age-related changes in Tree Structure and Function**”

Plant community function can be estimated by respiration, the amount of litter-fall. etc. (MNY method: M=mass, N=number, Y= yield by K. Hozumi (statistical model)

→ Plant defense is changed with tree size to some extent.
due to an increase of leaf area per land area

Short-term exchange student (Ms, Yu Wailin) will join us to study on Cauli-flower plants under herbicide pressure

Abstract

Changes in herbivory and resource availability during a plant's development should promote ontogenetic shifts in resistance and tolerance, if the costs and benefits of these basic strategies also change as plants develop. We proposed and tested a general model to detect the expression of ontogenetic tradeoffs for these two alternative anti-herbivory strategies in *Raphanus sativus*.

We found that ontogenetic trajectories occur in both resistance and tolerance but in opposite directions. The juvenile stage was more resistant but less tolerant than the reproductive stage.

The ontogenetic switch from resistance to tolerance was consistent with the greater vulnerability of young plants to leaf damage and with the costs of resistance and tolerance found at each stage.

We posit that the ontogenetic perspective presented here will be helpful in resolving the current debate on the existence and detection of a general resistance–tolerance tradeoff.

ハツカダイコン

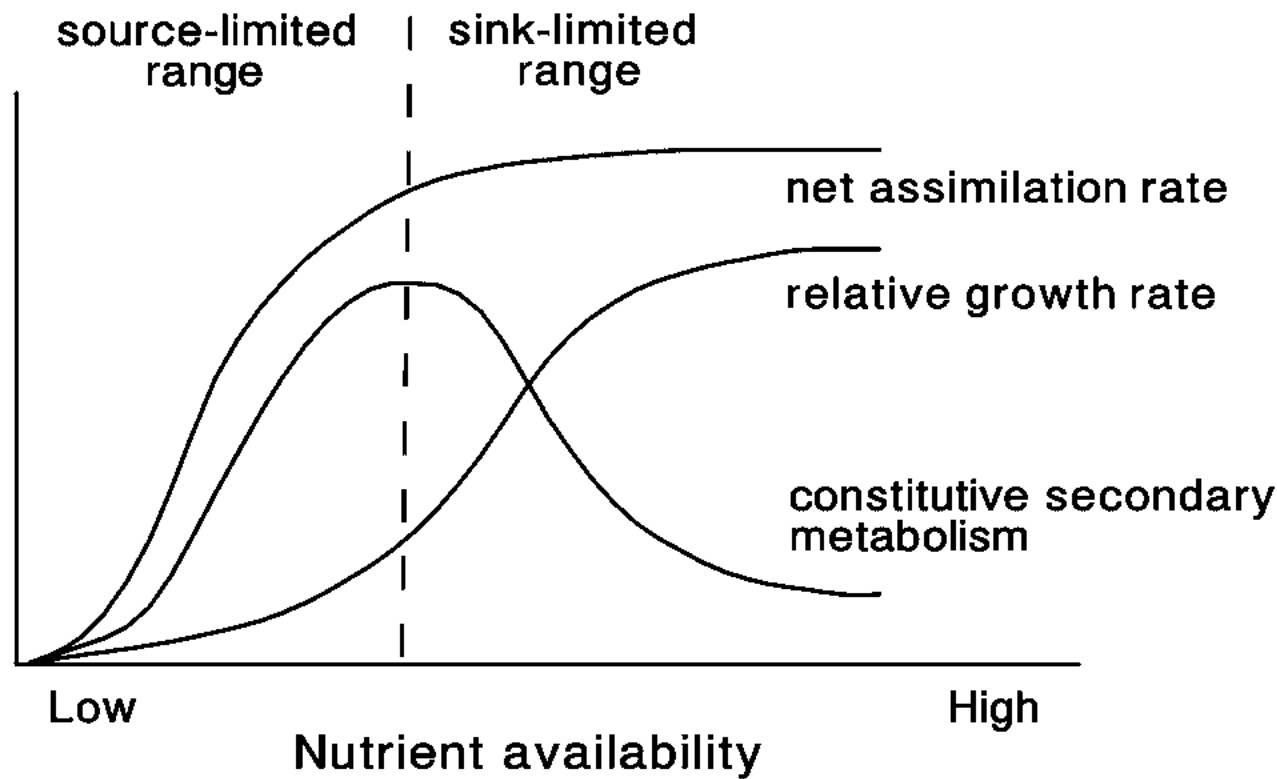
Raphanus sativus

アブラナ科

→カラシ油配糖体
(質的防御)

self-incompatible: 自家不和合の

昆虫だけではなく、シカ、ウサギなども食べる！



- ・隣接個体との光競争に勝つためには成長が重要だし、食べられないためには防御が重要。状況によって、どちらにより多く投資すれば良いかが異なり、その結果防御への資源投資比率が異なる。
- ・もともとCNB仮説が防御物質の挙動を説明できないケースが多いため代替仮説として提案。
- ・防御に使える炭素の量を説明できるが、個々の物質の量までは説明できない。(→結果の解釈)

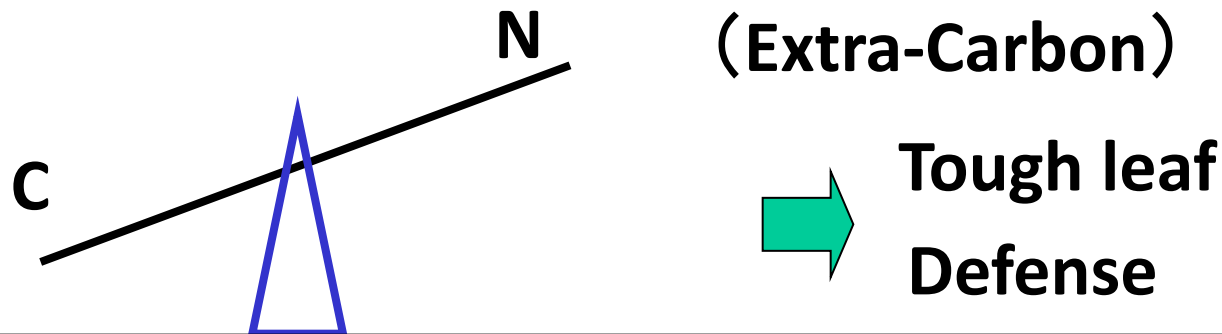
Carbon-Nutrient balance (CNB) hypothesis

(Bryant et al. 1983)

**Poor
Nutrient**

Environment

Elevated CO₂

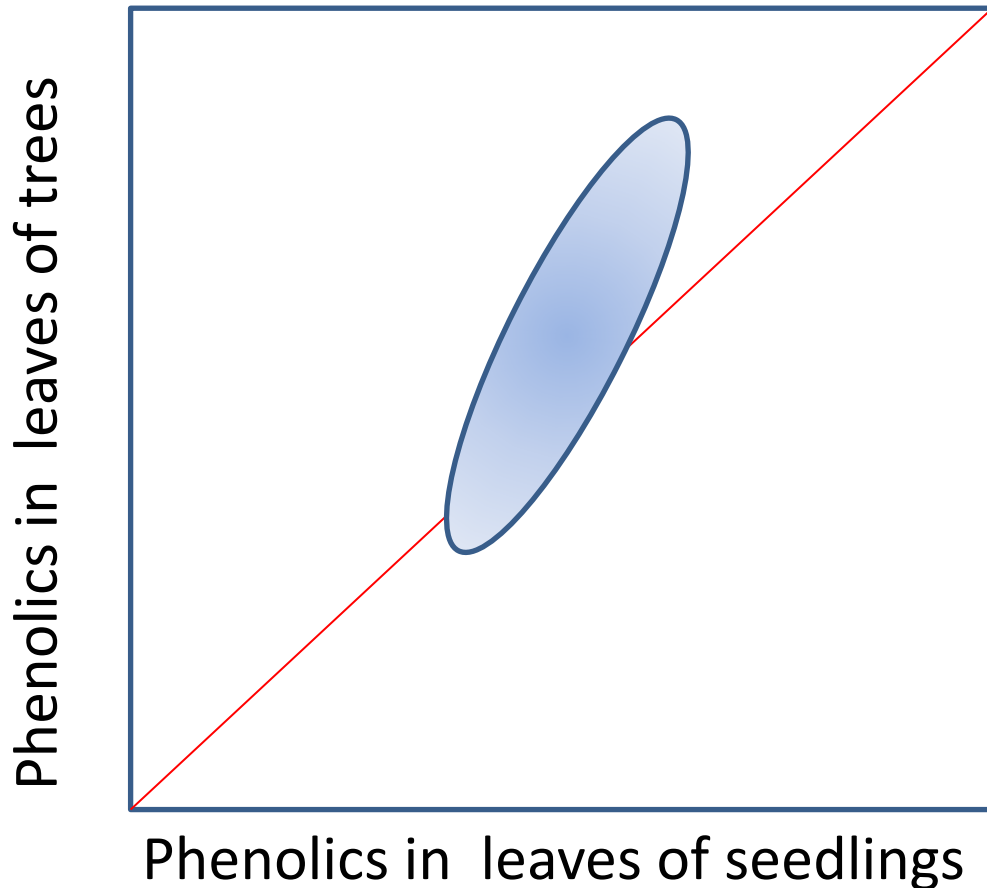


例えば栄養塩が不足していれば、植物体内では炭素が過剰になる。このような場合、余った炭素からタンニンなどCHOのみで構成される(Nを含まない)防御物質を合成すれば過剰な炭素を効率よく利用できる。

→CNB仮説は防御に使える炭素の量を説明できるが、個々の物質の量までは説明できない。

A comparison in defense chemicals between seedlings and adult trees in 6 species

(Koike et al. 2004 Trans action Jpn For Soc)



How about
change in
defense chemicals
in seedlings &
saplings grown
under elevated O₃?

個体サイズが大きくなれば、利用出来る資源量が増え防御へ投資できる物質も増加！？(GDB, CNB)

Water stress (physiology + morphology)

耐乾性 (Drought **resistance**)

回避性 (avoidance ; escape)

- ① stomata response
- ② dehydration
- ③ leaf shedding

耐性 (**tolerance**) → acclimation

- ① osmotic potential
- ② small sized leaf + cuticle increase
(tolerance is large in big body)

浸透調節 (Osmotic adjustment)

These are after Levitt (1972)

Objectives of this study

To test for the existence of an ontogenetic tradeoff between tolerance and resistance we constructed a model based on the mean genotypic difference in the expression of resistance and tolerance between ontogenetic stages.

In this model, the correlation between ontogenetic differences in resistance and ontogenetic differences in tolerance allows the assessment of the magnitude and direction of ontogenetic change in one strategy relative to the degree of change in the alternative strategy

Hypothesis

- (i) ontogenetic differences of vulnerability to leaf damage;
- (ii) the presence of ontogenetic trajectories in plant resistance and tolerance;
- (iii) whether **fitness** costs of resistance and tolerance are maintained throughout plant ontogeny;
適応度: 親と同じ形質を持つ子供の数で評価
- (iv) whether there are ontogenetic tradeoffs in the expression of both strategies, using the proposed model.

To assess the impact of defoliation on plant fitness we quantified the number of flowers and fruits produced by plants from each treatment. We estimated the total number of seeds from the mean seed number of 20 randomly chosen fruits per plant multiplied by the total number of fruits.

Finally, we calculated seed set (W) for each plant as $W = \frac{1}{4} \text{ seeds/flowers}$, and we considered this variable as the expression of one component of plant fitness.

Under the assumptions that:

(a) herbivore pressure is constant and has significant impacts on plant fitness throughout ontogeny;

(b) tolerance and resistance are costly and redundant strategies during plant development; and

(c) costs of both tolerance and resistance are equivalent throughout ontogeny, we should expect to see that when the ontogenetic trajectory in one strategy is expressed as a function of its benefits on fitness, an ontogenetic trajectory with the opposite trend is expressed

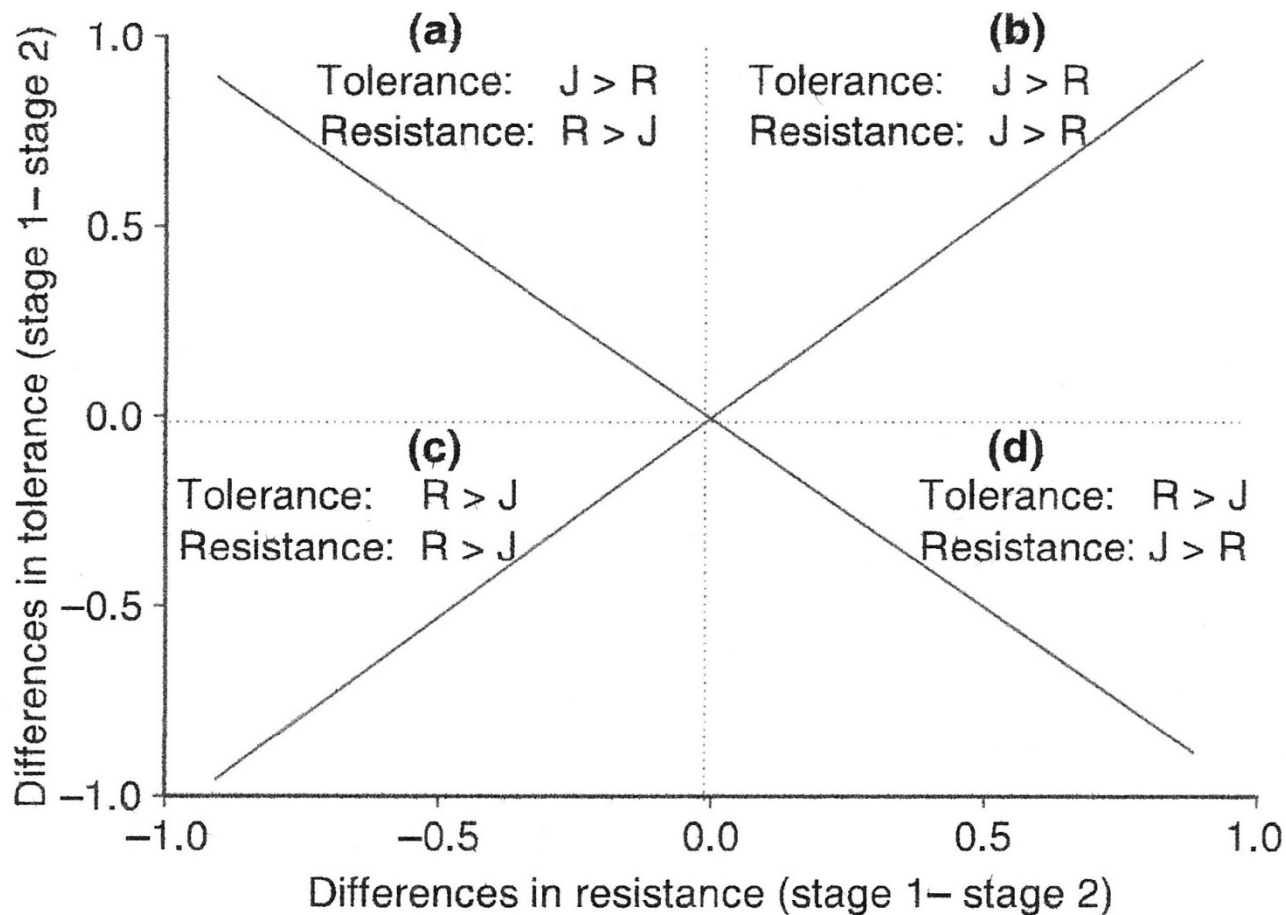


Fig. 1 Proposed graphic model to interpret the simultaneous ontogenetic changes in tolerance and resistance at two ontogenetic stages (e.g. J = Juvenile, R = Reproductive).

For interpretation of correlations between the mean genotypic ontogenetic differences in tolerance and resistance

Materials and Methods → Factorial design,

We produced four different groups:

- 1) control (C), in which no leaf damage was applied;
- 2) juvenile (J)-- 50% of each leaf area was removed when plants had four fully expanded leaves and started to expand their fifth leaf;
- 3) reproductive (R)-- 50% of each leaf area was removed when the plants had produced their first five to 10 flowers, and
- 4) both (J · R)-- plants were defoliated by removing 50% of each leaf area at the juvenile stage and 50% of subsequently produced leaves when plants reached maturity (i.e. every leaf was damaged only once).

Tolerance when plants were damaged at the juvenile (TJ) and reproductive (TR) stages was estimated for each family as the **difference in fitness** between the damaged group (either J or R)

and

the control (non-damaged) group (C) ($TJ \frac{1}{4} WJ$) WC , $TR \frac{1}{4} WR$) WC),

thus positive values indicate greater tolerance than smaller and negative values

Fig 2. Vulnerability of plants to defoliation when damaged at the juvenile or reproductive stage, and consecutively during both stages. Different letters represent significant differences among treatments ($P < 0.05$). Seed set was damaged

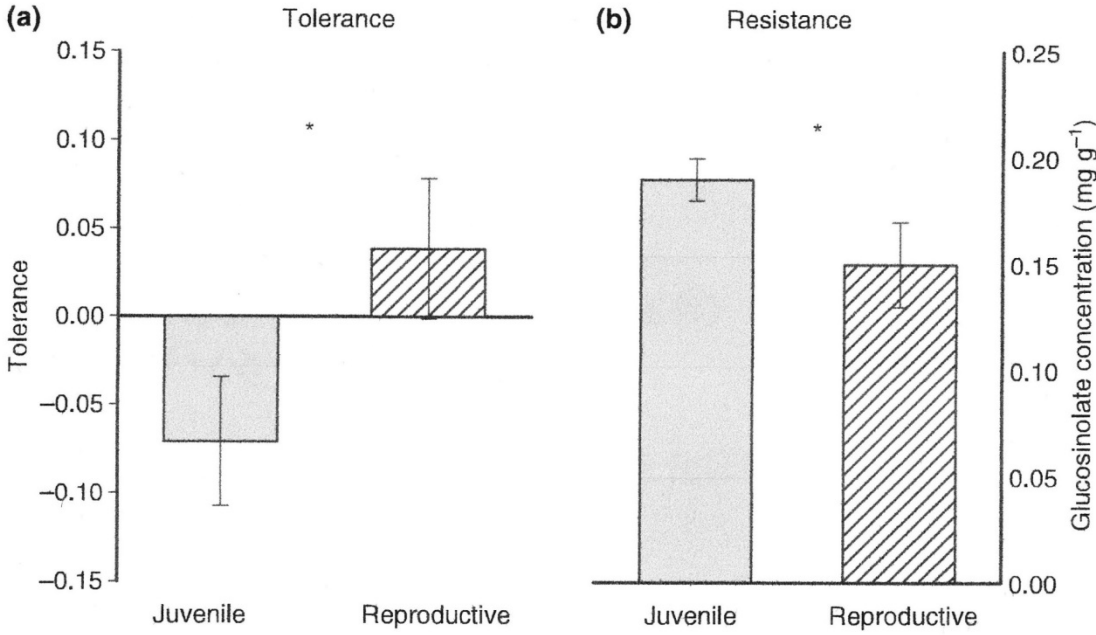


Fig 3 Ontogenetic changes in: (a) plant tolerance to defoliation; (b) resistance. Asterisks represent significant differences between ontogenetic stages ($P < 0.05$).

To describe the ontogenetic trajectories in resistance and tolerance and their degree of correlation, we calculated the

mean genotypic ontogenetic change (D) in total glucosinolate concentration (G) as $DG \frac{1}{4} (\text{Family average } GJ))$

(Family average GR),

and the degree of ontogenetic change in tolerance (T) as $DT \frac{1}{4} (\text{Family average } TJ))$ (Family average TR).

We then used a regression analysis to describe the joint pattern of ontogenetic variation in tolerance and resistance (JMP, SAS Institute 2001).

Responses of relative growth rate, net assimilation rate, and constitutive secondary metabolism across a gradient of nutrient availability as predicted by the growth–differentiation balance hypothesis. In source-limited plants a positive correlation is predicted between growth and secondary metabolism, while in sink-limited plants the correlation is predicted to be negative (modified from fig. 1 of Herms & Mattson, 1992).

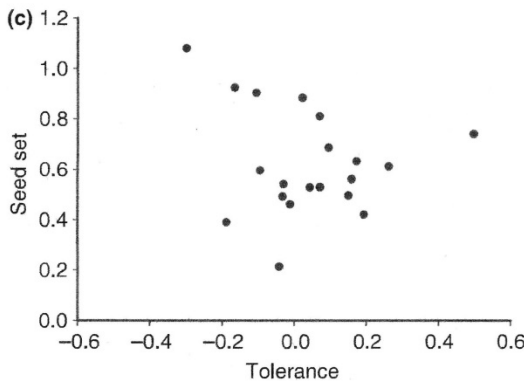
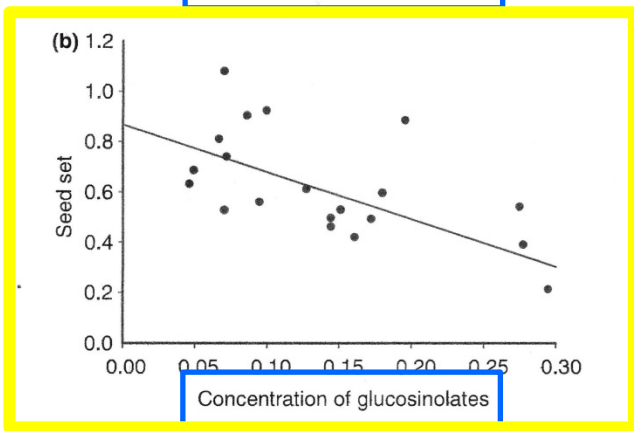
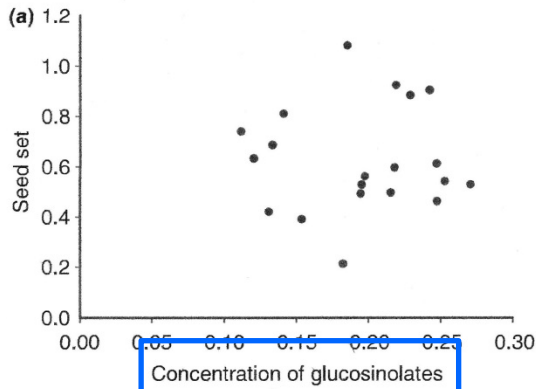


Figure 4 Costs of resistance at the juvenile stage (a) and at the reproductive stage (b) and cost of tolerance at the reproductive

Fig 4 Seed set & glucosinolate

a) Costs of resistance at the juvenile stage

b) at the **reproductive stage**

c) cost of tolerance at the reproductive stage

of *Raphanus sativus*.

カラシ油配糖体

(mustard oil glycosides) は、
グルコシノレート (**glucosinolates**)

→配糖体から糖が外れ、

イソチオシアネートやニトリルなど

毒性のある物質になる

Fig 5 Ontogenetic tradeoff between resistance and tolerance in *Raphanus sativus*. Positive values along the axes represent greater levels of resistance and/or tolerance at the juvenile stage relative to the reproductive stages, whereas negative values are interpreted as greater tolerance and/or resistance at the reproductive than at the juvenile stage.

Conclusion

This model is certainly a simplified version of the trends that the simultaneous expression of tolerance and resistance can follow throughout plant ontogeny, which can be more complex if factors such as resource availability, plant vigour, and the simultaneous expression of different resistance traits are considered.

Predictions of the model should differ for annual and perennial plants, given the differences in their apparency and probability of damage, the diversity of herbivore species attacking them, storage abilities:

(i) their reproductive strategy

i.e. iteroparous : 多回繁殖性 or

semelparous: 一回繁殖)

(ii) the proportion of their biomass allocated to tissues attacked by herbivores