Course contents:	**1. Insect abundance and distribution: species-area relationships. Diversity of forest insects in relation to tree species, feeding guilds, and to the history of forest stands. Invasive species in forestry: definitions, concepts, and applications.** **2. Classification of the outbreaks and related examples. Population dynamics: demographic growth versus mortality. Population cycles in different types of forest ecosystems.** **3. Ecological factors affecting the populations of forest insects. Effects of climate and temperature, including climate change. Mechanisms of resistance developed by the host plants and adaptations of the insects (host physiology). Role of competition and of natural enemies in population regulation.** **4. Principles of integrated pest managements based on the knowledge of the insect ecology. Prevention, direct and indirect control, economic assessment of costs and benefits of IPM in forestry.**

Eco-physiological models explaining the plant defenses

- hierarchical resource allocation (Waring & Pitman 1985)

- carbon/nutrients (C/N) balance hypothesis (Bryant et al. 1983

- growth/differentiation balance hypothesis (Loomis 1932, Lorio 1986, Herms & Mattson 1992)

Hierarchical resource allocation (Waring & Pitman 1985)

Priority of carbon allocation

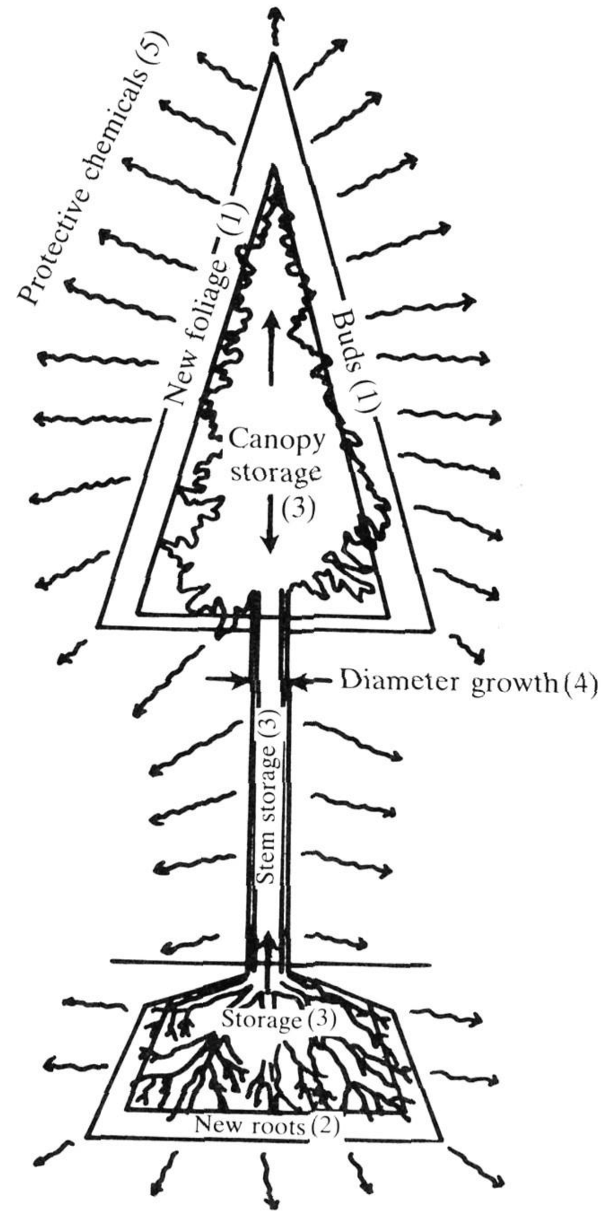


FIG. 3.20. Likely priorities for the allocation of carbohydrate in lodgepole pine. Priorities are numbered from 1 (highest) to 5 (lowest). (from Waring and Pitman 1985).

carbon/nutrients (C/N) balance hypothesis (Bryant et al. 1983

Assumptions

Plant Growth: mainly nutrient dependent

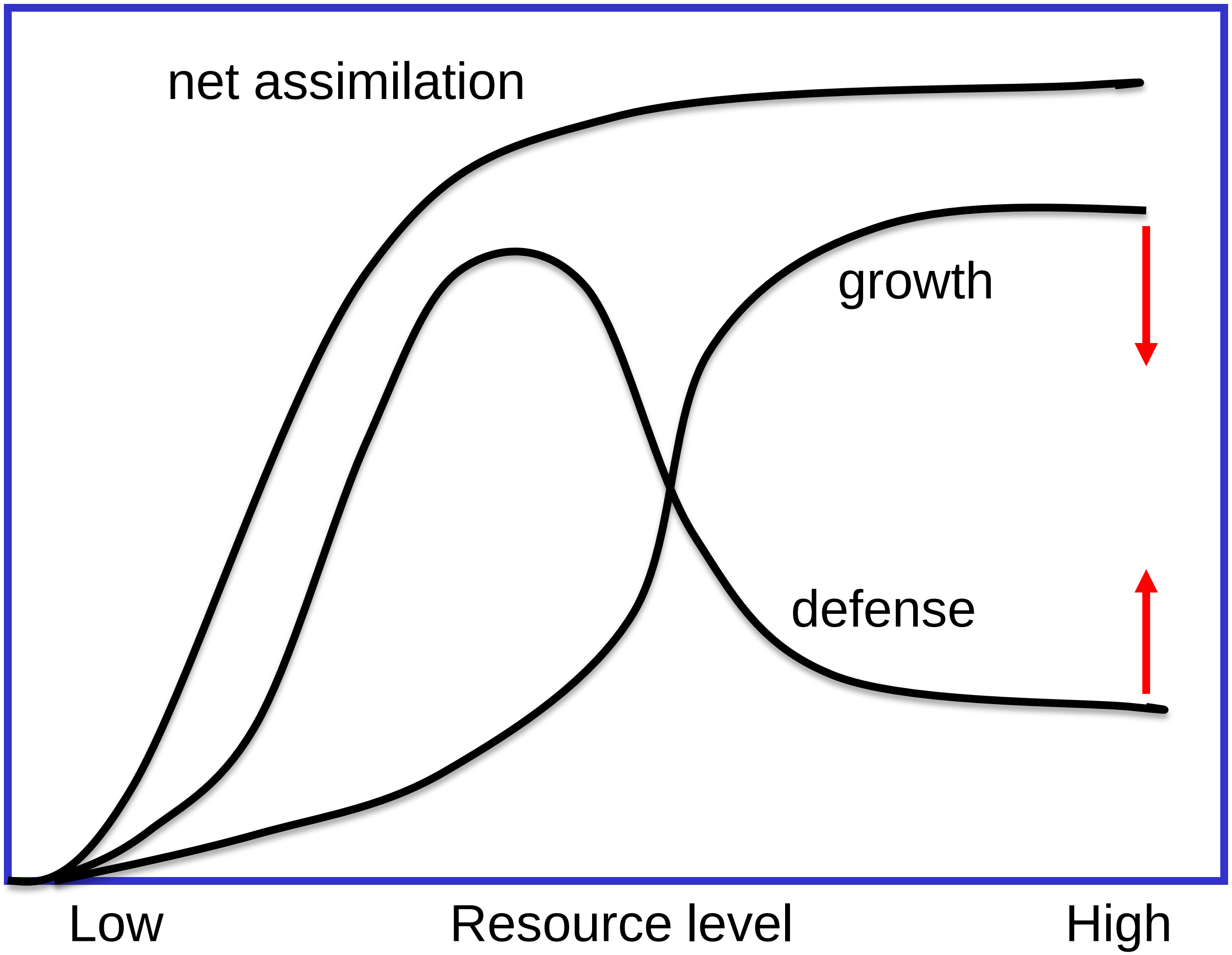
Plant Defense: mainly carbon dependent

Hypothesis

Availability of nutrients favours the growth

Growth/differentiation balance hypothesis (Loomis 1932, Lorio 1986, Herms & Mattson 1992)

Trade-off concept



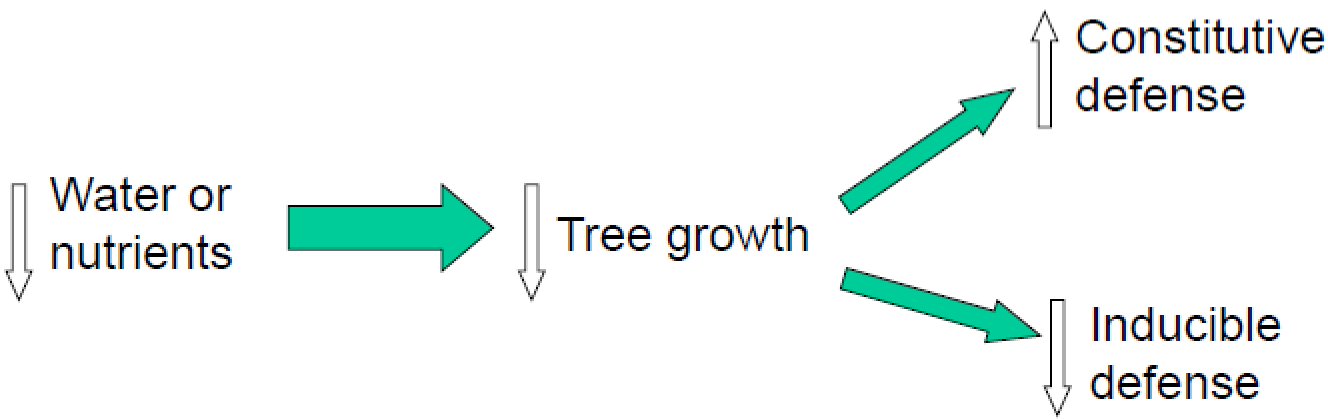
Constitutive defenses: always present

Induced defenses: produced on demand

- Localized
- Systemic
- Extended to other individuals: priming

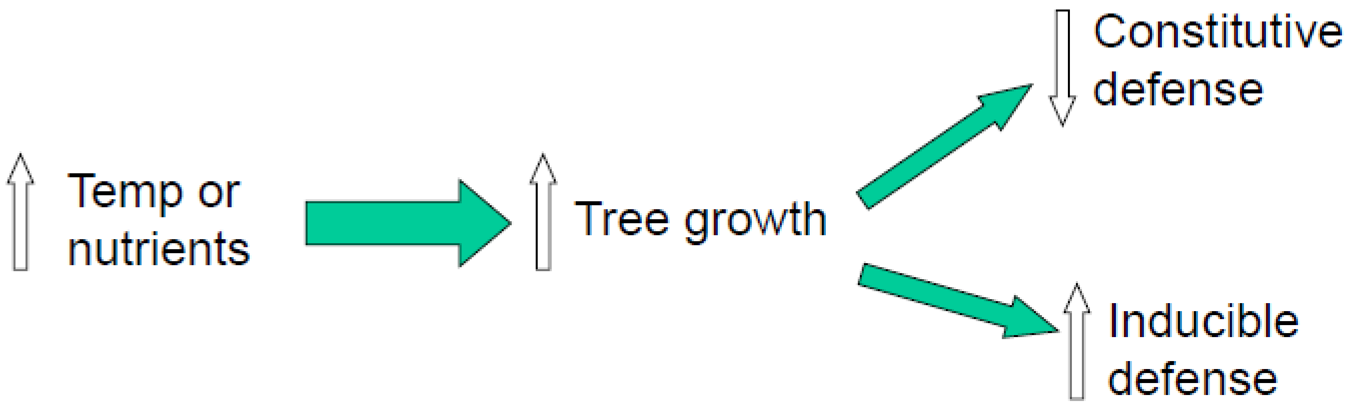
Why variable effects?

1. Nonlinear physiological responses
2. Constitutive vs. inducible defenses



Temperate conditions, temperature not limiting, Lombardero et al. 2000

Where temperature is limiting (high elevation and latitude)



Model predictions vary according to the geographical region

Induced defenses and reaction time

Delayed induced resistance (DIR)

Rapid induced resistance (RIR)

Hypersensitive reaction (HR)

RIR/DIR of Norway spruce to the attack of Ips typographus and associated blue-stain fungi.

Identification of a gene responsible of terpene synthesis and associated with traumatic resin canals.

Induction of the same reaction by application of methyl jasmonate.

Ralph et al.
2006

Hypersensitive reaction of willow midge

Hoglund et al. 2005

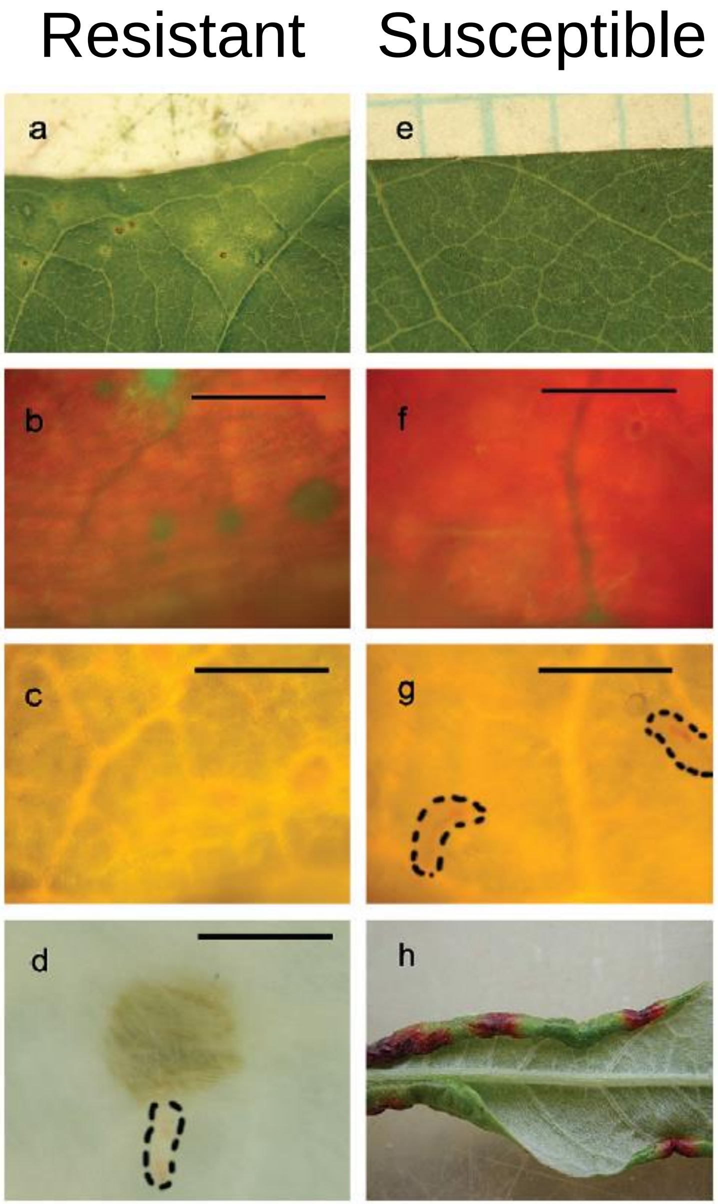


Fig. 2. Induced responses of *Salix viminalis* leaves attacked by neonate *Dasineura marginemtorquens* larvae. Plant responses on the resistant RML genotype (a–d) and the RFL genotype (e–g) show presence of lesions and markers for hydrogen peroxide in the case of RML and absence of lesions and markers in the case of RFL. The plant response on susceptible genotypes (h) shows formation of young galls on the underside of the leaf. Lesions were visible at the upper side of the leaf in stereomicroscope in the case of RML (a) but absent in the case of RFL (e). Green spots, indicating presence of hydrogen peroxide, were visible in fluorescence microscopy with DCFH staining in the case of RML (b) but absent in the case of RFL (f). The same tissue under light microscopy showed the presence of lesions in RML (c) and the absence of lesions in RFL (g). In the case of RFL (g) the presence of two larvae is indicated with dashed lines. Brown lesions indicated the presence of hydrogen peroxide in RML (d) with a non-fluorescent DAB staining. The presence of a young larva is indicated with a dashed line (d). Scale bars represent 0.5 mm.

Defense strategy of *Pinus sylvestris* against bark beetle associated fungi

Caterina Villari

Conifer resistance to pests and pathogens

Constitutive:

- general defenses normally present in the tree
- act to repel or inhibit invader access

↓

- resin ducts
- lignin
- stone cells
- low amount of secondary metabolites (*e.g.*, phenolics, terpenoids and alkaloids)

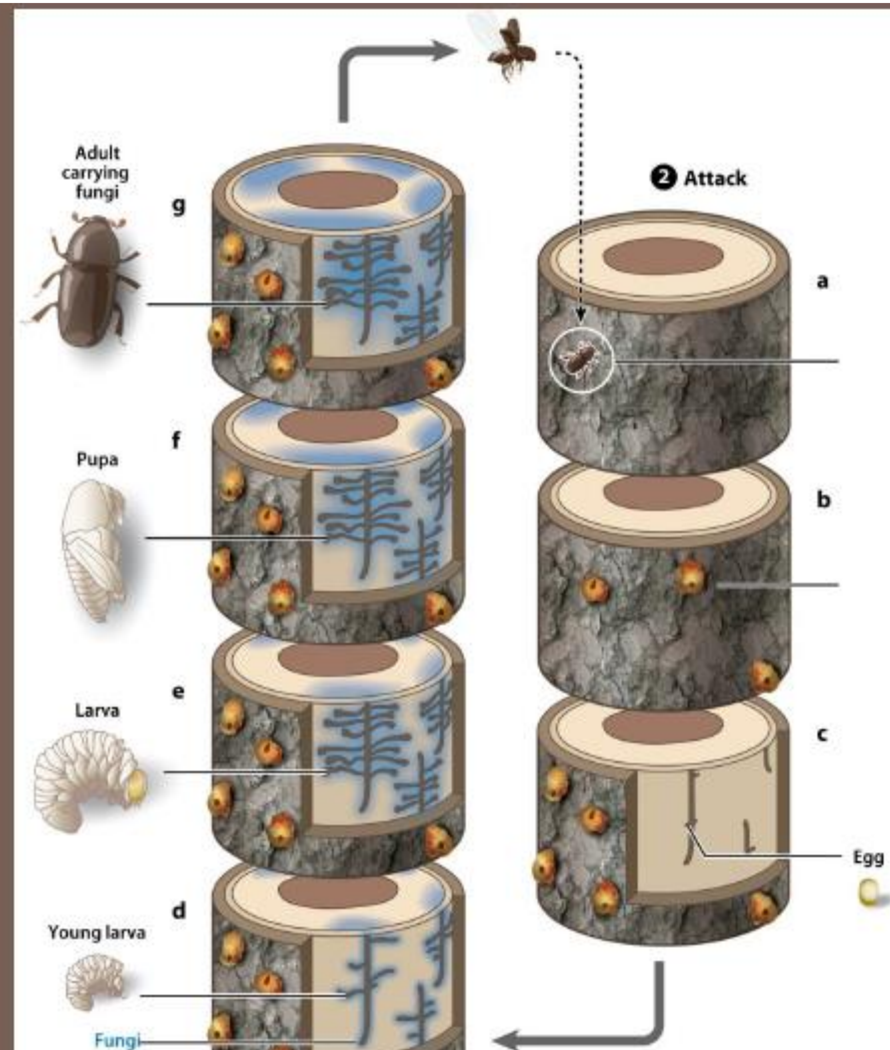
Induced:

- triggered by invaders access
- act to kill or compartmentalize the agent once an attack has begun

↓

- traumatic resin ducts
- qualitative and quantitative changes of secondary metabolites
- hypersensitive autonecrosis
- synthesis of pathogenesis-related proteins

Association between bark beetles and symbiotic fungi



Six DL, Wingfield MJ. 2011. Annu. Rev. Entomol. 56:255–72

Benefits for the beetles:

- Nourishment for the larvae (*e.g.* sterols, vitamins)

  → Ambrosia fungi, non pathogenic

- Interaction with the host plant defenses

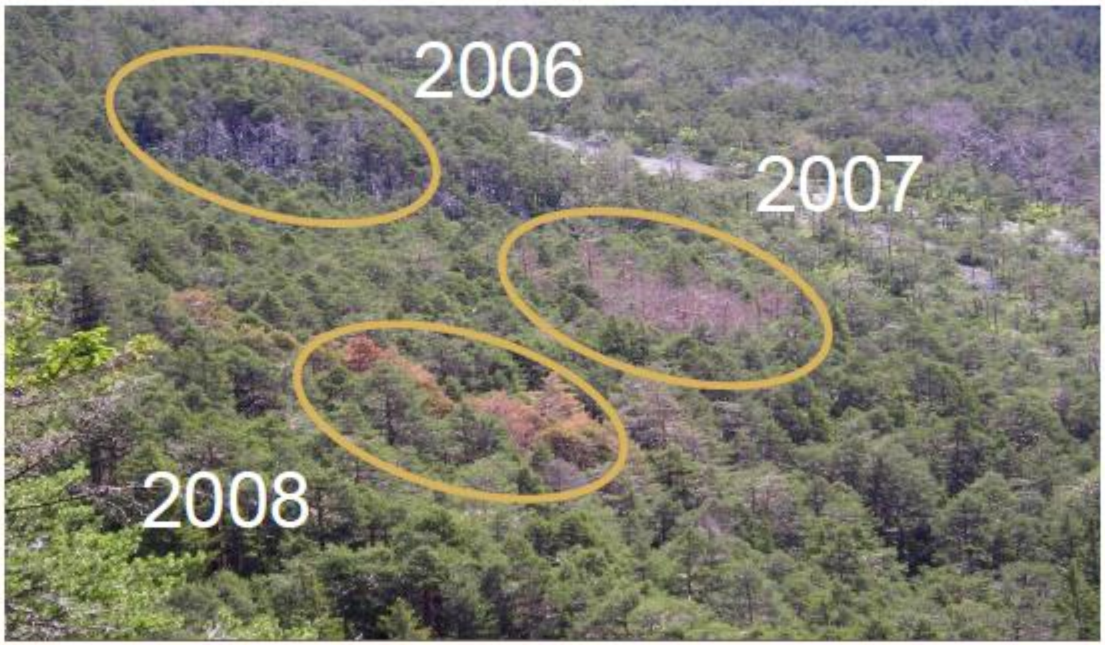
  → Blue-stain fungi, more or less aggressive pathogens

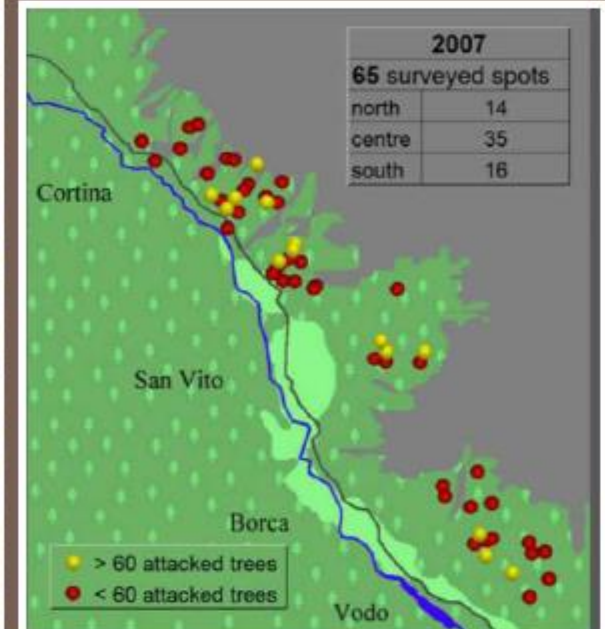
Model system: *Ips acuminatus* – associated fungi complex

- Small bark beetle attacking thin barks of Scots pine

- Associated with the nutritional ambrosia fungus *Hyalorhinocladiella macrospora* and the blue-stain fungus *Ophiostoma clavatum*

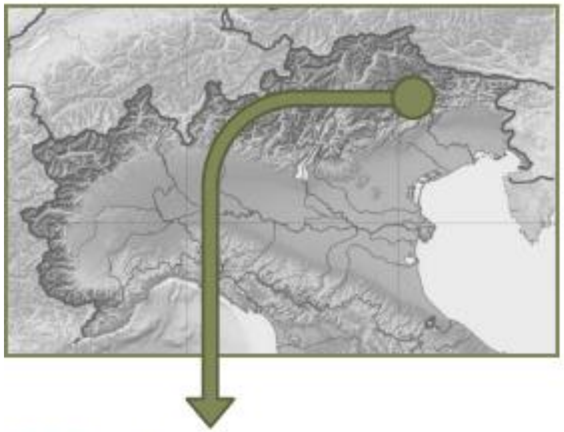
- Spatially structured populations

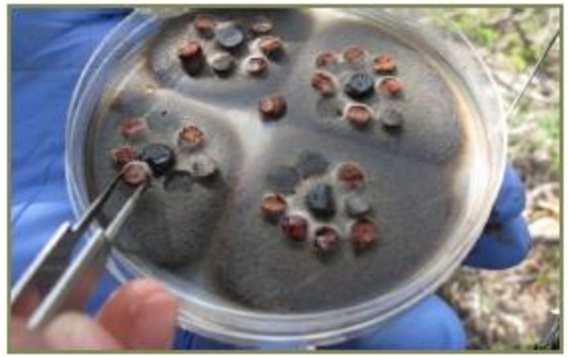




Colombari et al. 2013, AFE

M&M Experimental site and inoculation treatments





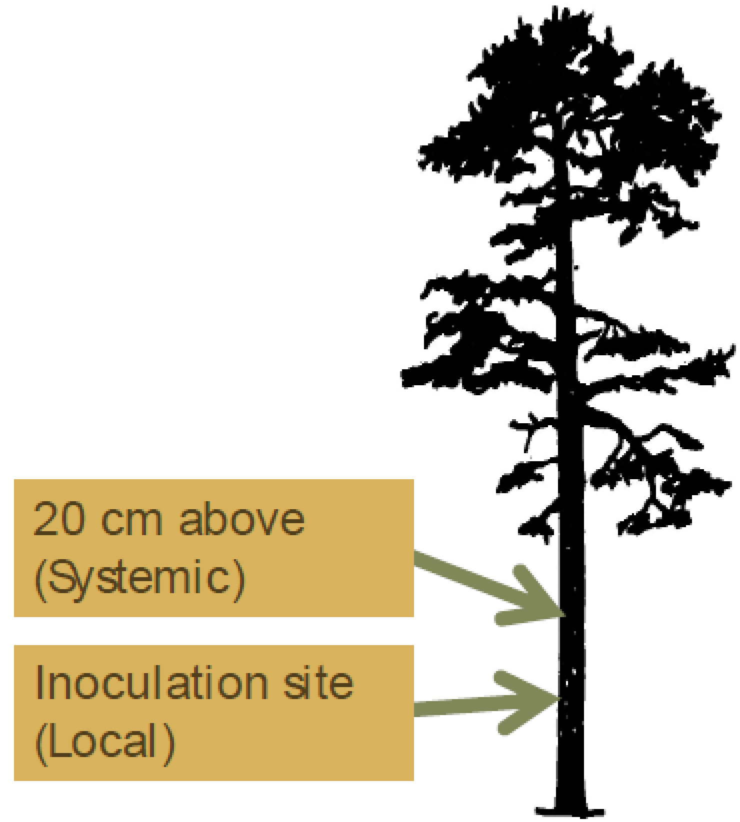
50 plants
San Vito di Cadore (BL)
1105 m a.s.l.

- 4 treatments
- 3 weeks
- Lesion measurement

M&M Secondary metabolites analyses

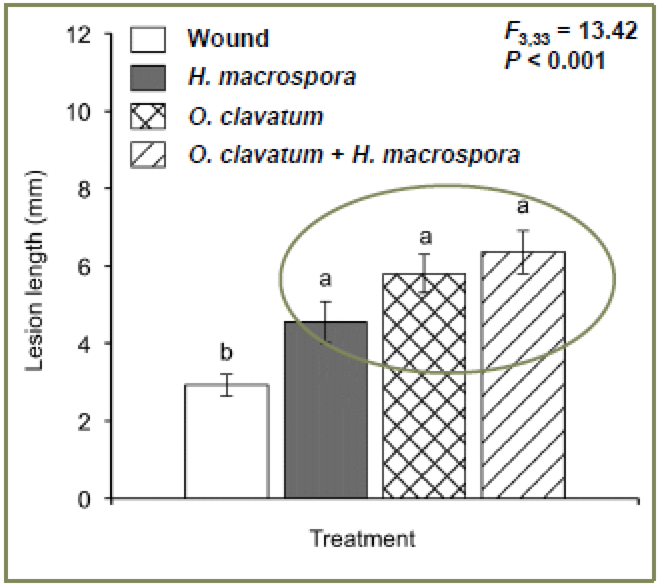
- Constitutive (time zero, T_0)
- Induced (3 week after, T_1)
- HPLC, LC-MS, and GC-MS analyses
- Phenolic compounds, lignin and terpenoids

Inducible $\Delta = T_1 - T_0$

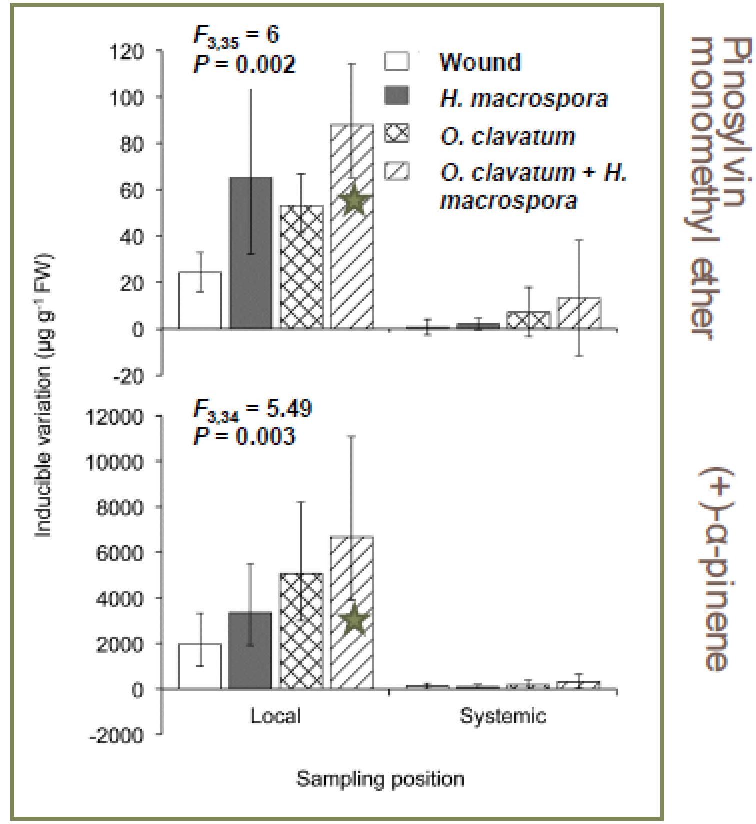


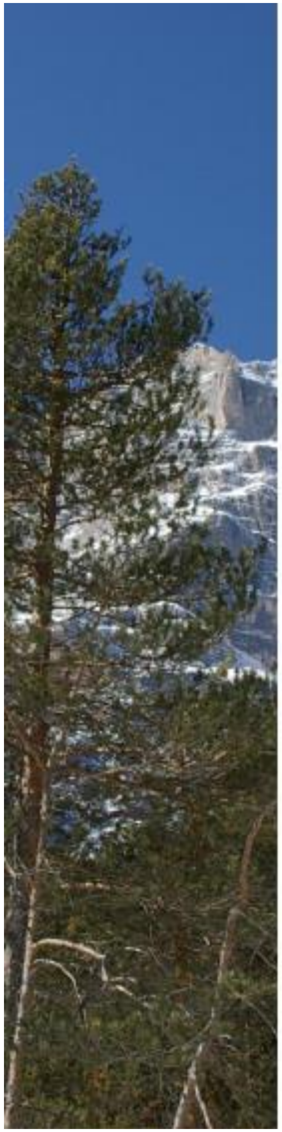
Results

Lesion length and secondary metabolites response

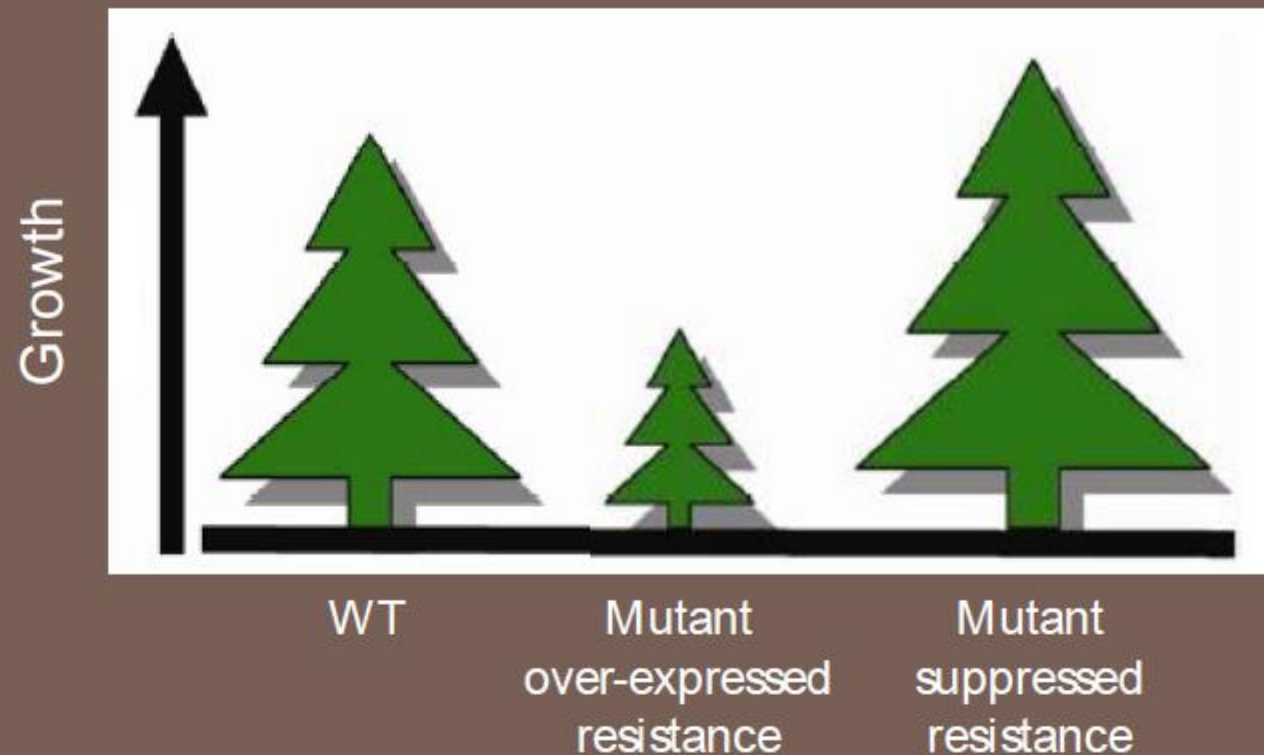


- High inducible response of stilbenes, flavonoids and terpenoids
- Strong position effect ($P < 0.0001$)
- No treatment effect ($P > 0.01$)

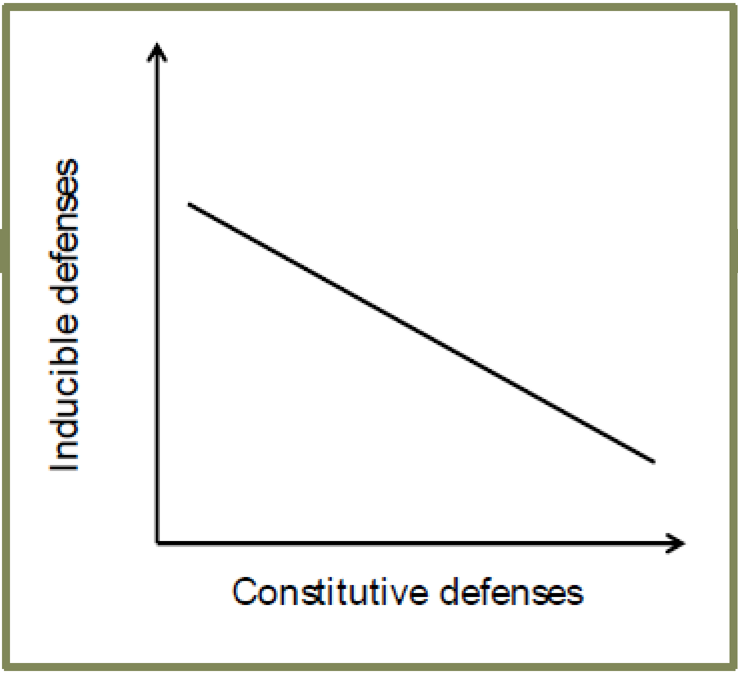


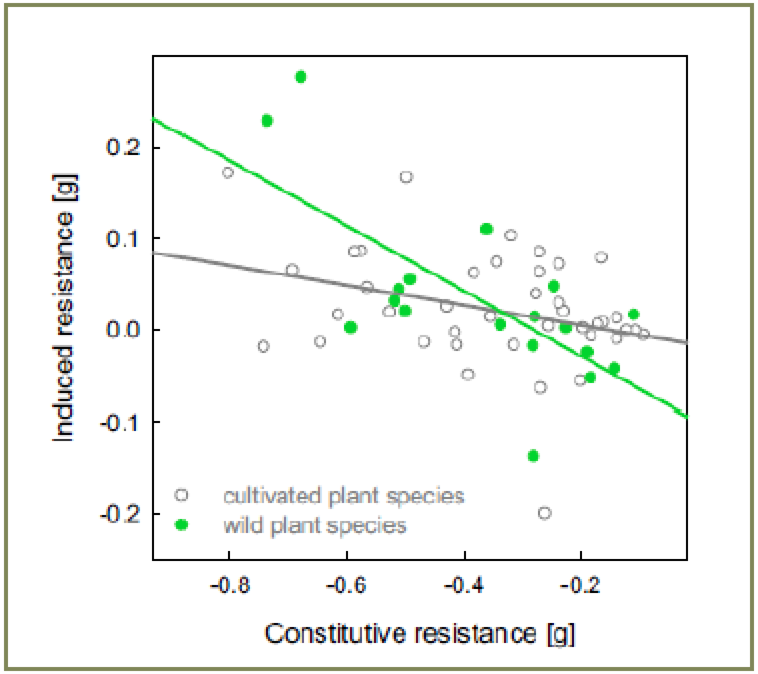


Resistance is energetically expensive!!



Trade-offs between constitutive and induced defenses, Karban & Myers 1989



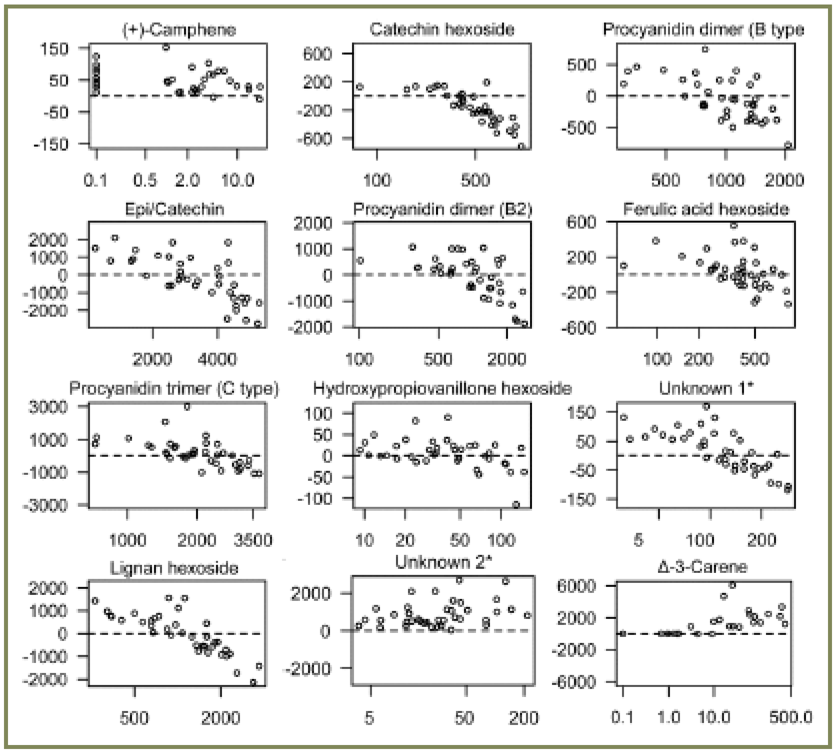


Tested often in herbaceous plants, *e.g.* Kempel et al. 2011, but seldom in conifers, and only for generic traits

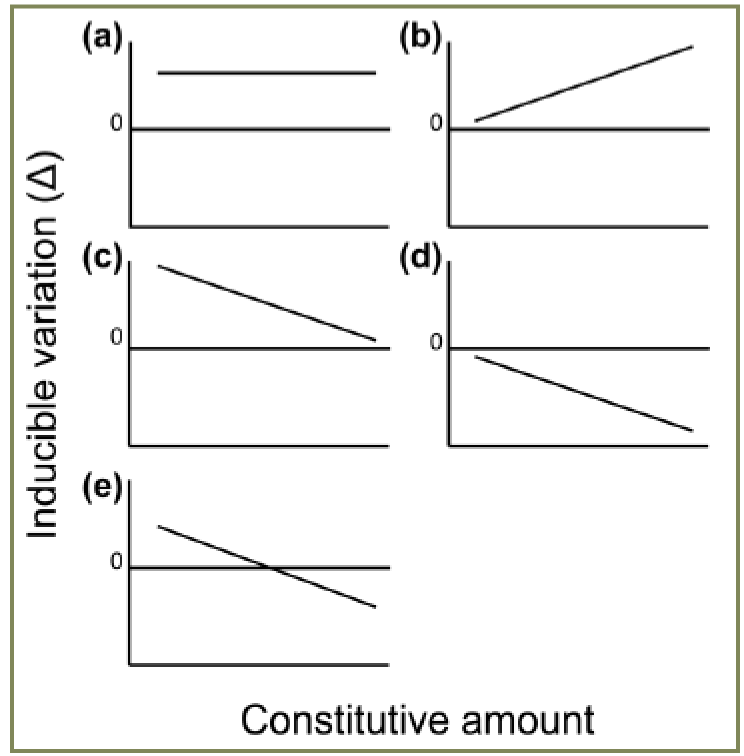
Results

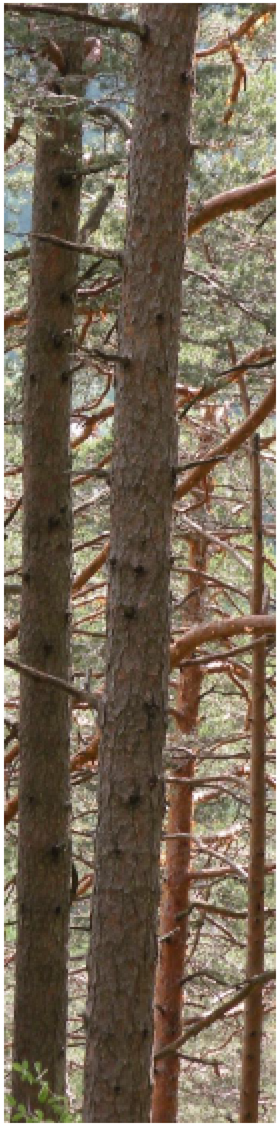
Trade-offs between constitutive and induced metabolites

Real correlation patterns



Response types





Conclusions

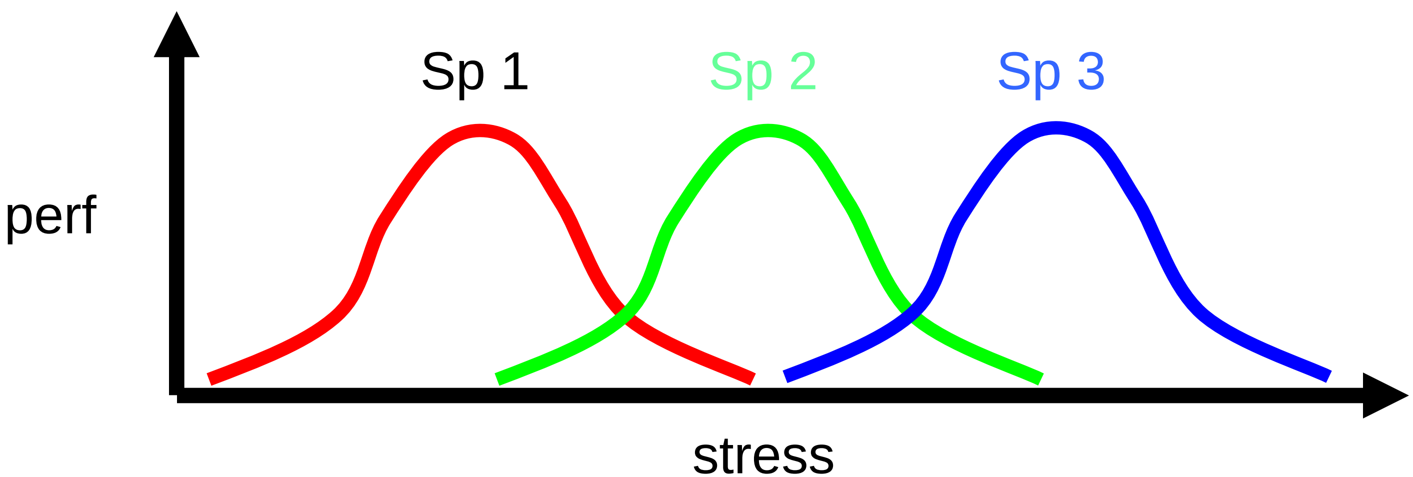
- Scots pine has a varied and complex defense chemistry whose individual components are not functionally redundant (no trade-offs)

- Only constitutive specialized metabolism is influenced by tree ring growth

- Compounds that are usually not considered as involved in defense showed a significant reaction, suggesting a role in plant responses to biotic stressors

Stressful time for the plant stress – insect performance hypothesis (Larsson 1989, Koricheva et al. 1998, Huberty and Denno 2004)

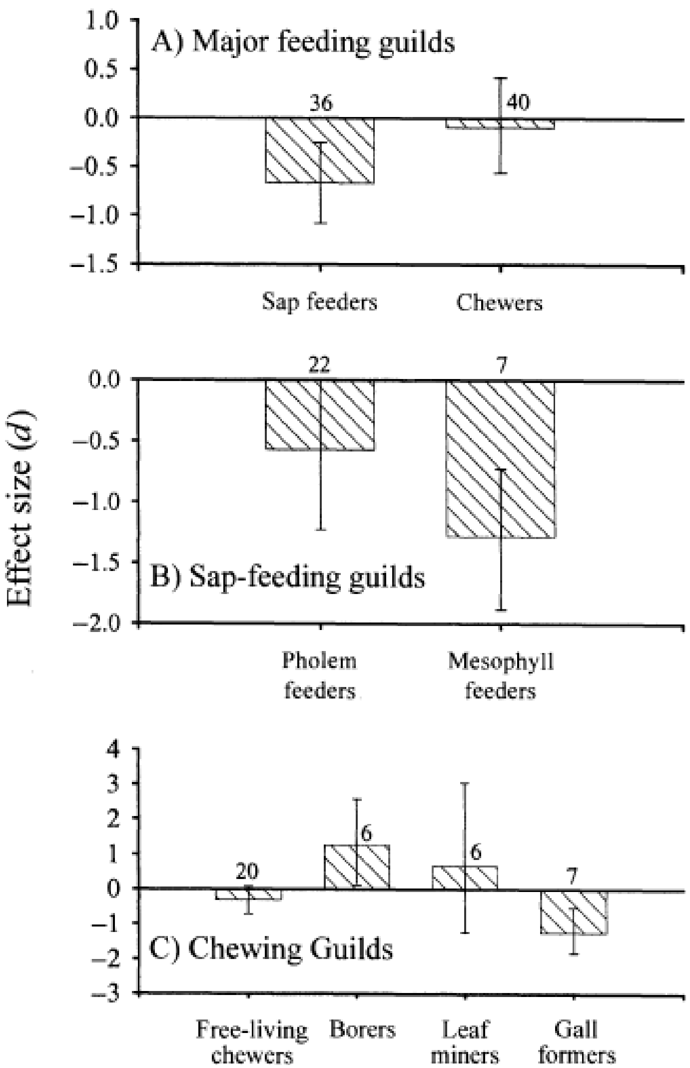
Positive and negative outcomes depending on the susceptibility window



Ecology, 85(5), 2004, pp. 1383–1398

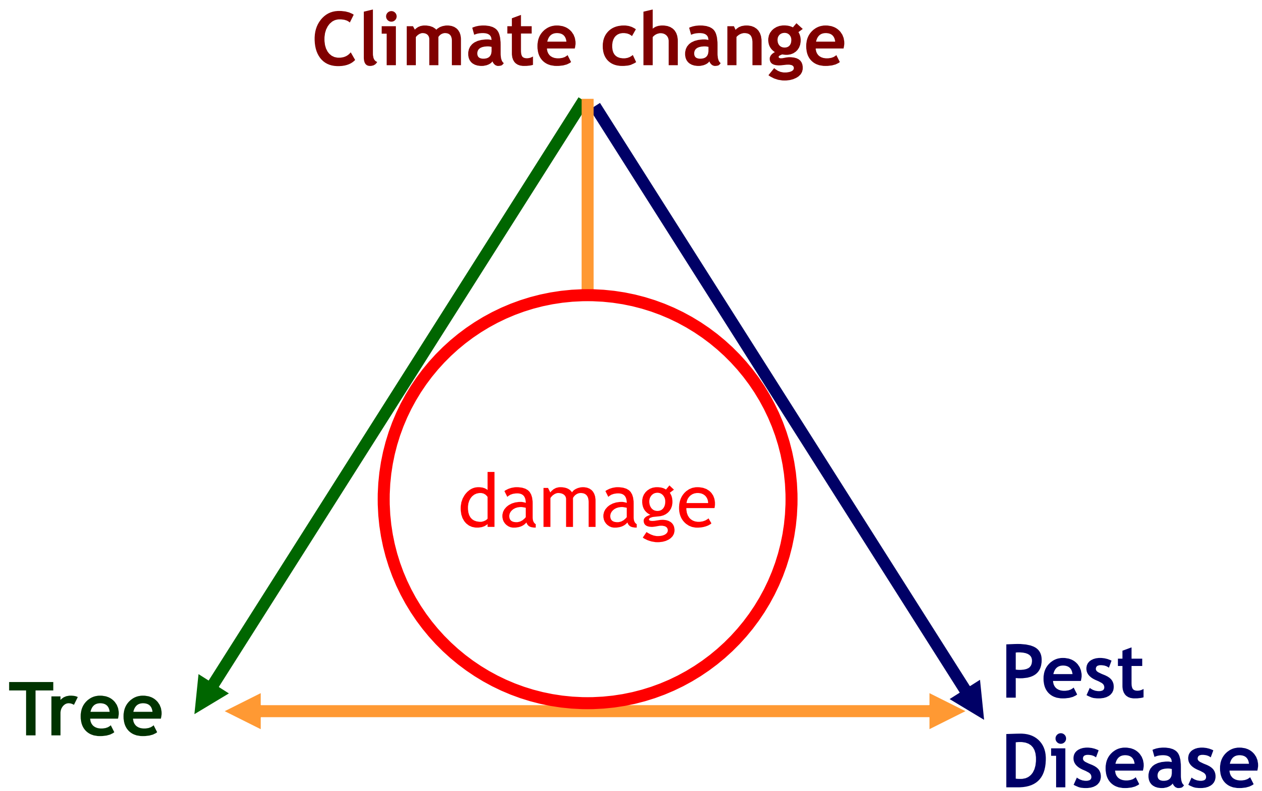
PLANT WATER STRESS AND ITS CONSEQUENCES FOR HERBIVOROUS INSECTS: A NEW SYNTHESIS

ANDREA F. HUBERTY[1] AND ROBERT F. DENNO



Contrasted effects of plant water stress on the overall performance of different feeding guilds of phytophagous insects

Drought ➔ Indirect effects on pest infestation through changes in host plant quality or resistance



Damage = result of climate effect on tree + pest + tree × pest interactions

Will more severe or frequent drought result in higher pest and disease damage in forests ?

The relationship between water stress and tree susceptibility to pest and disease is still controversial (inconsistent experimental evidence)

➔ A meta-analysis of the international scientific literature

A meta-analysis is an ‘analysis of analyses’: statistical methods to make generalisations from a series of experiments (published papers) in an unbiased, quantitative way

- *How large is the overall effect of a particular factor, across all studies ?*
- *Can this variation be explained by covariates ?*

Publication included in the meta-analysis if it met 6 criteria:

1. Comparison of damage (deformation, defoliation, growth loss, mortality
2. Quantified by mean, stdev and sample size
3. On a particular tree species
4. By a particular pest insect or pathogenic fungus
5. Between a control and a water stress treatment
6. Water stress quantified by the predawn leaf water potential (PL)

standardized Hedges' effect size

$$d = J_{N_C,N_S} \frac{Mean_S - Mean_C}{Stdev_{C,S}}$$

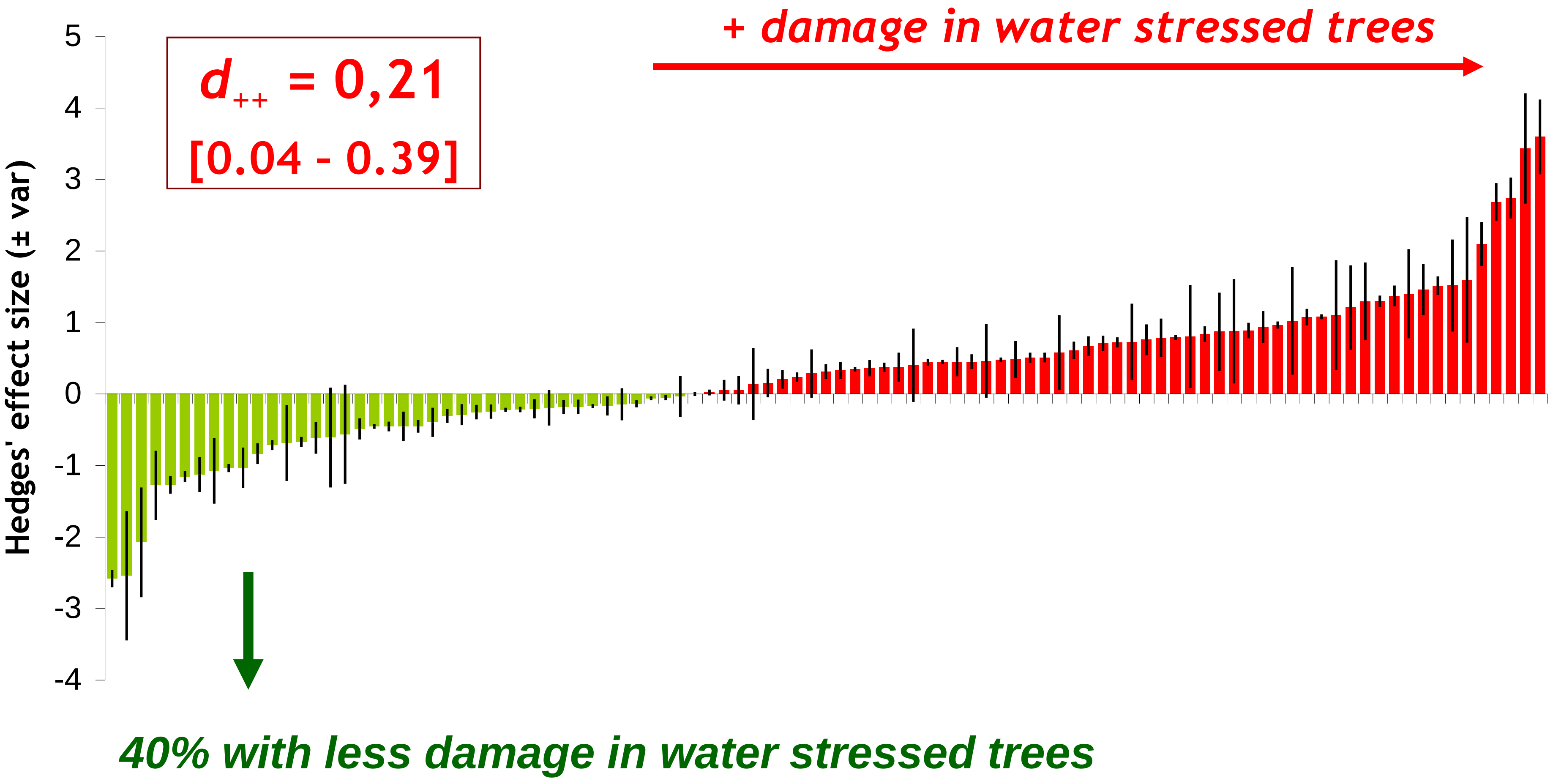
C = control group
S = water stress group

$$stdev_{C,S} = \sqrt{\frac{(N_C - 1) \times stdev_C + (N_S - 1) \times stdev_S}{N_C + N_S - 2}}$$

$$J_{N_C,N_S} = 1 - \frac{3}{4 \times (N_C + N_S - 2) - 1}$$

Total 99 studies

- 26 tree species
- 14 forest pathogens, 27 insect pests
- from 39 papers (>300 checked), published in 1975 - 2010



NO significant difference in response to drought

- between type of tree species:

broadleaves	(45)	$d_+ = 0.28$
conifers	(54)	$d_+ = 0.16$

- between tree age:

seedlings	(59)	$d_+ = 0.27$
mature trees	(40)	$d_+ = 0.13$

- between type of biotic agent:

fungi	(50)	$d_+ = 0.38$
insects	(49)	$d_+ = 0.07$

Definition of pest & disease functional groups

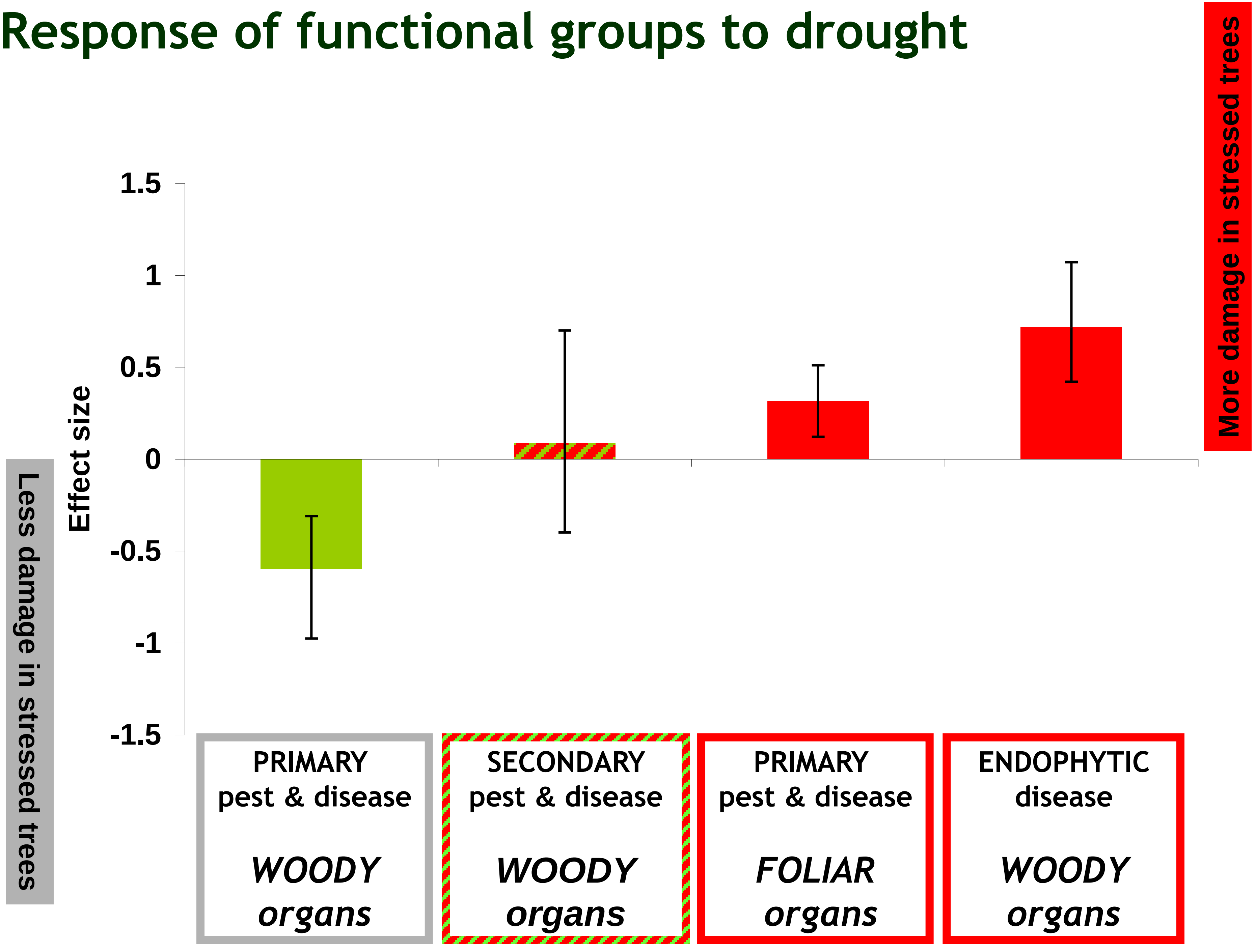
Primary pest & disease: able to infest healthy, vigorous trees
Secondary pest & disease: need stressed, weaken trees to survive/develo
Endophytic fungus: latent in healthy trees / pathogenic in stressed tr

pest and disease infesting **foliar organs** (leaves, needles, shoots) → photosynthesis

pest and disease infesting **woody organs** (bark, phloem, wood, roots) → structure

	Primary pest & disease	Secondary pest & disease	Endophytic fungus
FOLIAR organs Leaves Needles Shoots	***Neodiprion autumnalis*** ***Neodiprion sertifer*** ***Neodiprion fulviceps*** ***Malacosoma disstria*** ***Elatobium abietinum*** ***Corytucha arcuata*** ***Schizolachnus pineti*** ***Asphondylia spp.*** ***Lymantria dispar*** ***Chrysomela populi*** ***Leaf aphid sp.*** *Septoria musiva*	no study	no study
WOODY organs Bark Phloem Wood Roots	***Rhyacionia buoliana*** ***Pissodes validirostris*** ***Pissodes strobi*** ***Dioryctria sylvestrella*** ***Matsucoccus feytaudi*** *Phytophthora cinnamomi* *Armillaria ostoyae*	***Dendroctonus frontalis*** ***Ips acuminatus*** ***Oncideres cingulata*** ***Scolytus ventralis*** *Ophiostoma polonicum* *Ophiostoma ips* *Fusarium solani* *Thyronectria austro-americana* *Leptographium wingfieldii* *Leptographium yunnanense*	*Sphaeropsis sapinea* *Biscogniauxia mediterranea* *Botryosphaeria stevensii* *Botryosphaeria dothidea* *Cystospora chrysosperma*

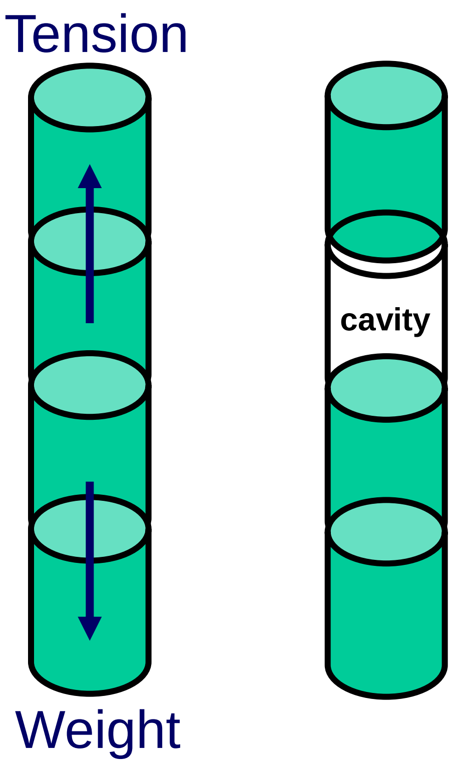
Response of functional groups to drought



Quantifying water stress intensity: Predawn Leaf potential

$PL_{control}$ PL_{stress} PL_{50}

Predawn leaf water potential at which 50% of hydraulic conductivity is lost due to xylem cavitation

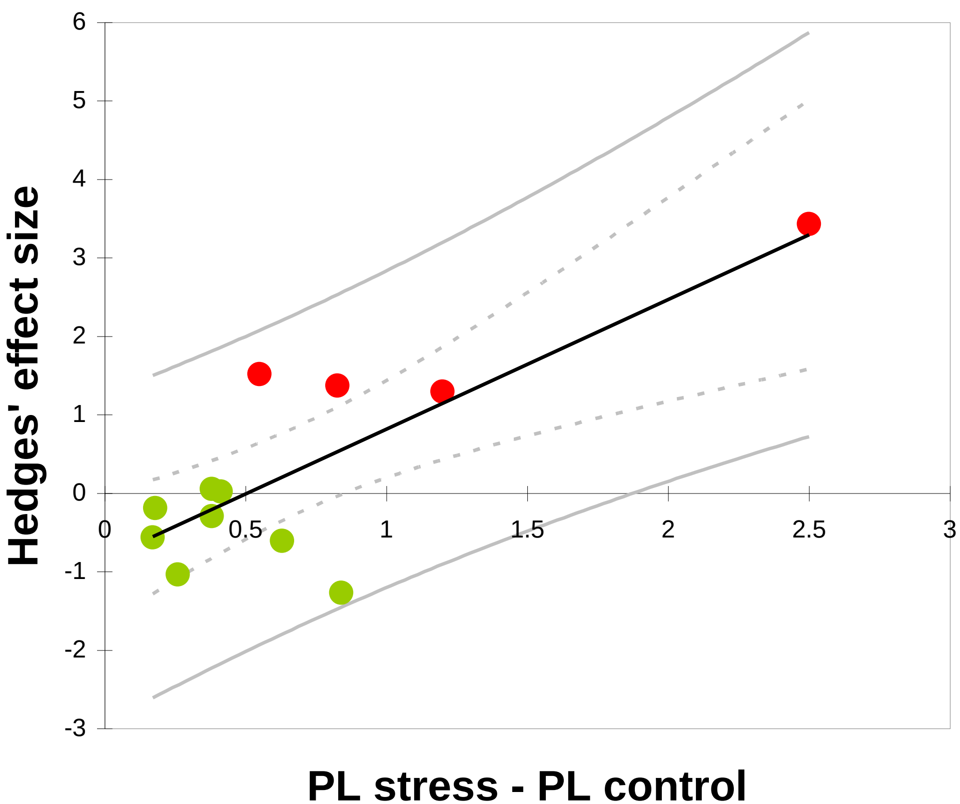


Water supply to leaves depends on maintaining an intact water column from roots to shoots. This hydraulic pathway is under tension. It is vulnerable to breakage through air embolism = xylem cavitation.

Tree species	PL 50
Populus euramericana	-1.34
Prosopis glandulosa	-1.50
Eucalyptus marginata	-1.82
Populus tremuloides	-1.96
Gleditsia triacanthos	-2.00
Betula pendula	-2.31
Larrea tridentata	-2.39
Quercus rubra	-2.43
Acer saccharum	-2.72
Quercus robur	-2.83
Populus nigra	-2.95
Pinus resinosa	-3.00
Pinus strobus	-3.00
Pinus ponderosa	-3.01
Pinus sylvestris	-3.23
Quercus pubescens	-3.30
Pinus taeda	-3.45
Picea abies	-3.69
Pinus pinaster	-3.73
Picea sitchensis	-3.85
Pistacia vera	-4.00
Quercus cerris	-4.50
Abies concolor	-5.00
Quercus suber	-5.30
Quercus ilex	-5.80

Drought resistance

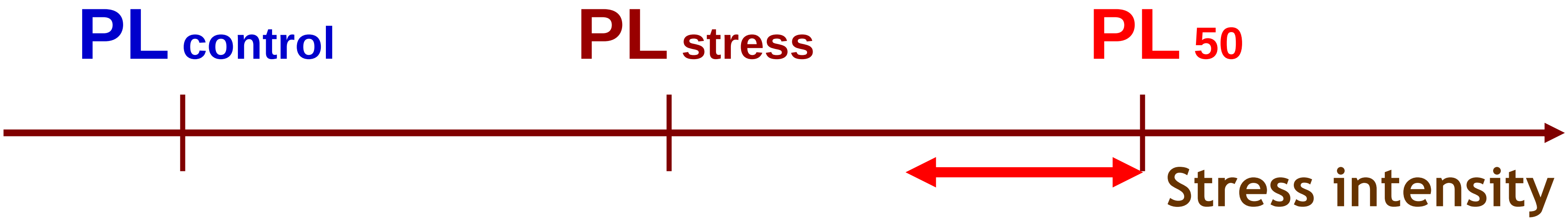
SECONDARY pest & disease
in WOODY tissues (bark, phloem, wood, roots)

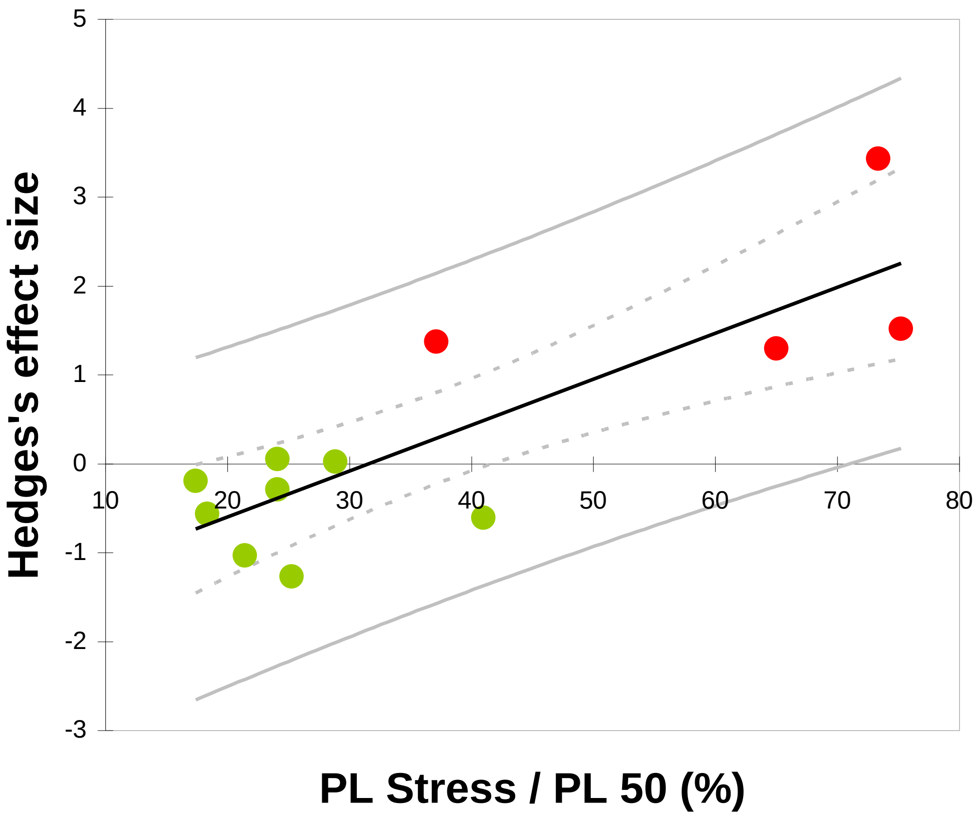


P = 0.002

R^2 = 0.63

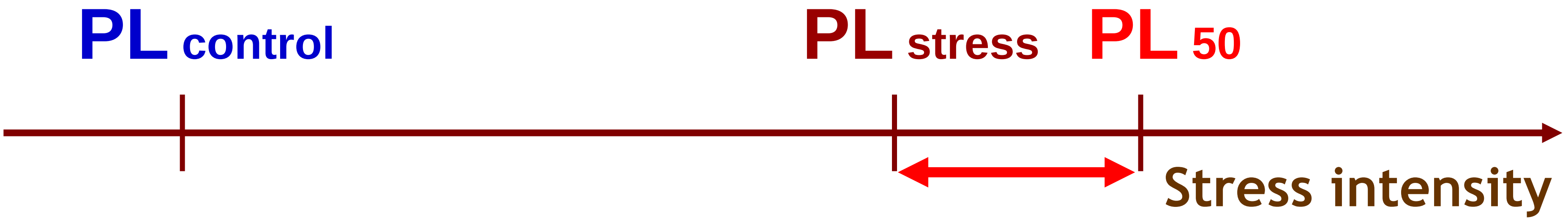
SECONDARY pest & disease
in WOODY tissues (bark, phloem, wood, roots)

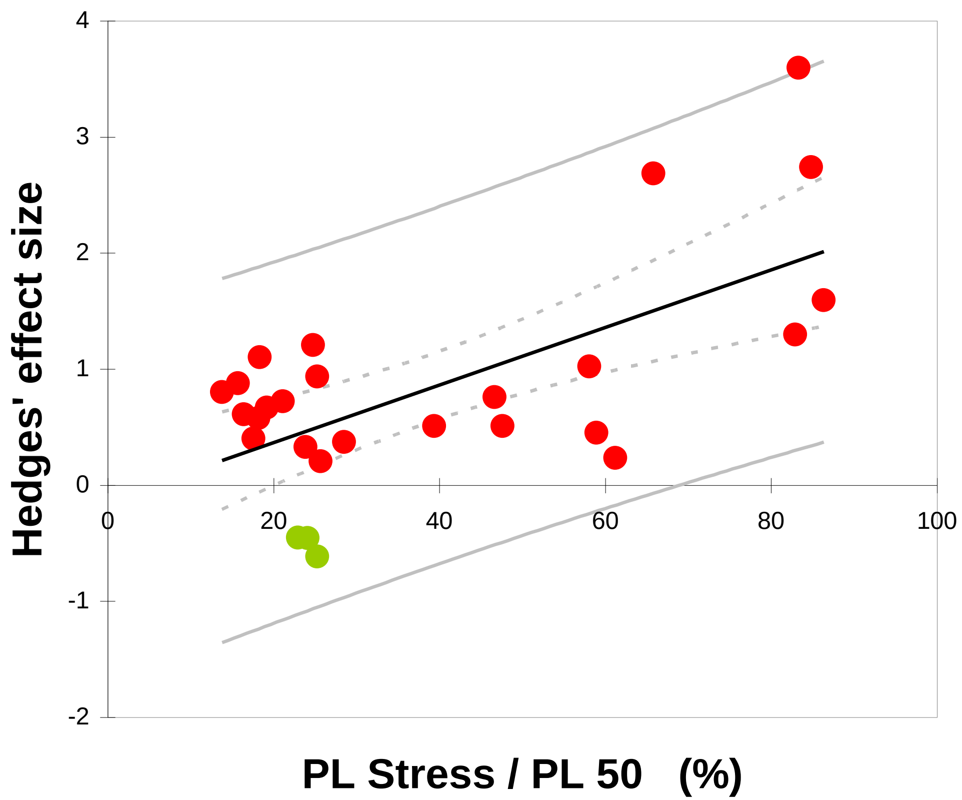




P = 0.001
R^2 = 0.68

ENDOPHYTIC fungi
in WOODY organs (bark, phloem, wood, roots)





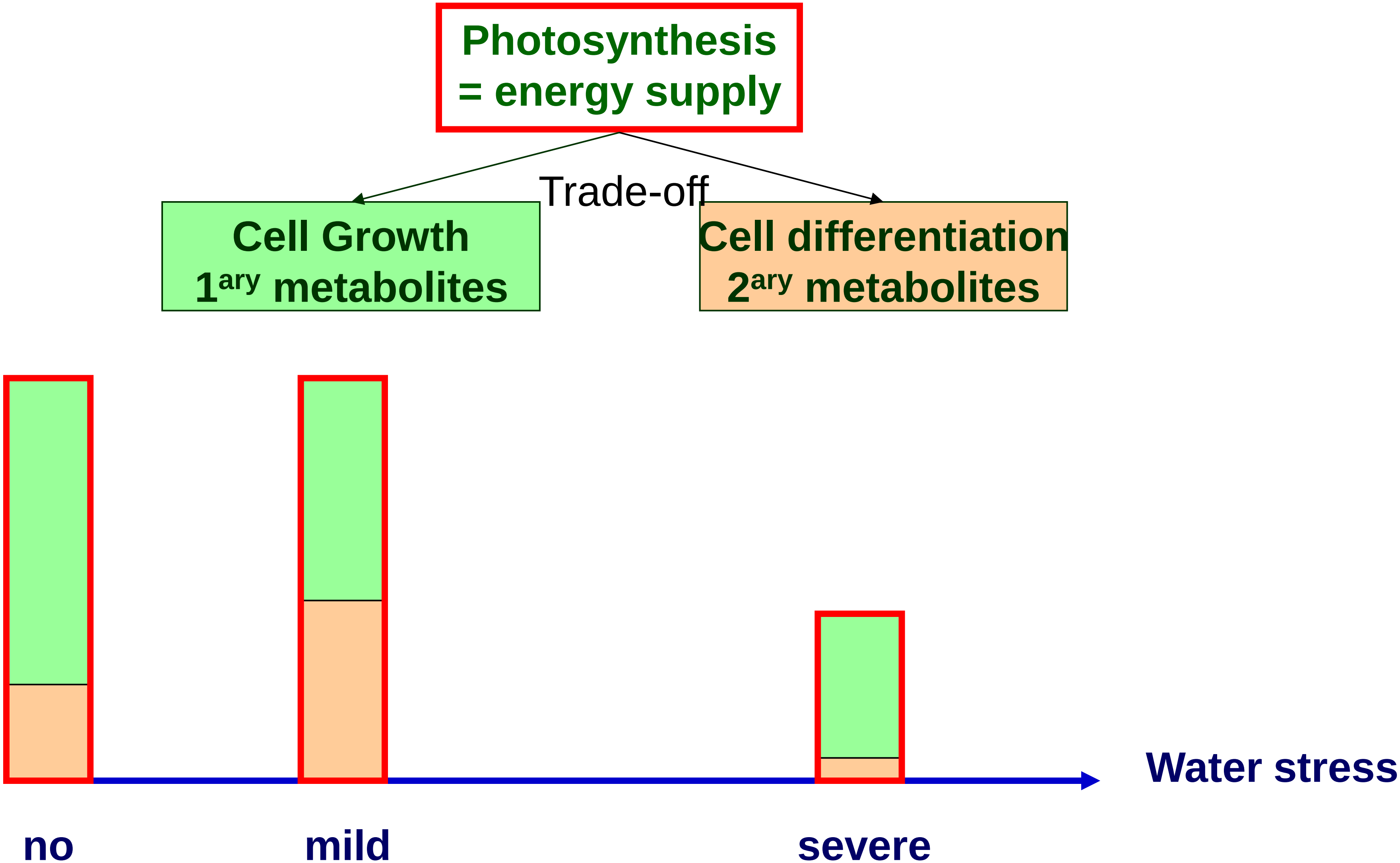
$P < 0.0001$

$R^2 = 0.42$

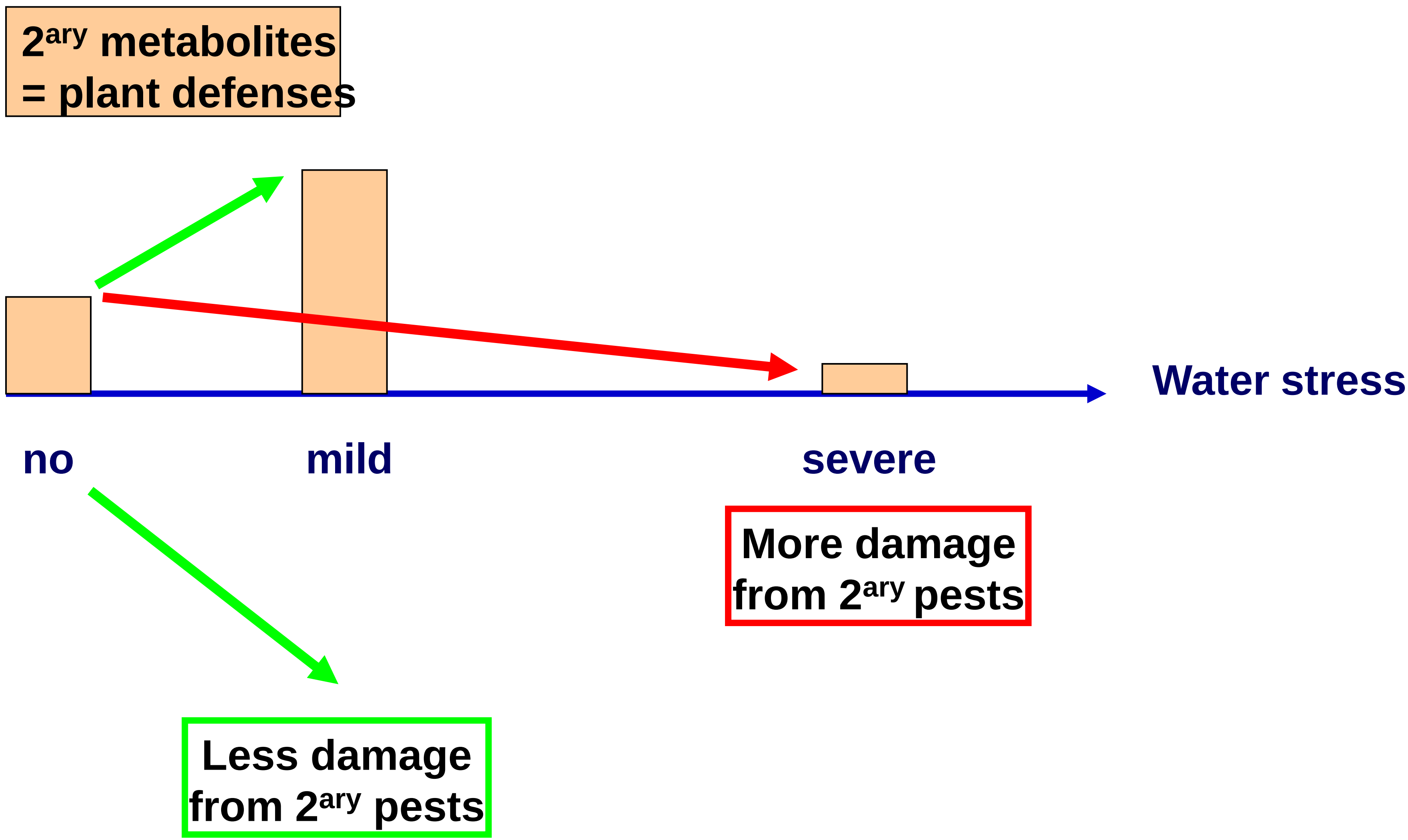
$R^2 = 0.21$ with (PL stress – PL control)

Response of secondary pest and disease to drought: the Growth - Differentiation Balance Hypothesis (GDBH)

Herms and Mattson 1992



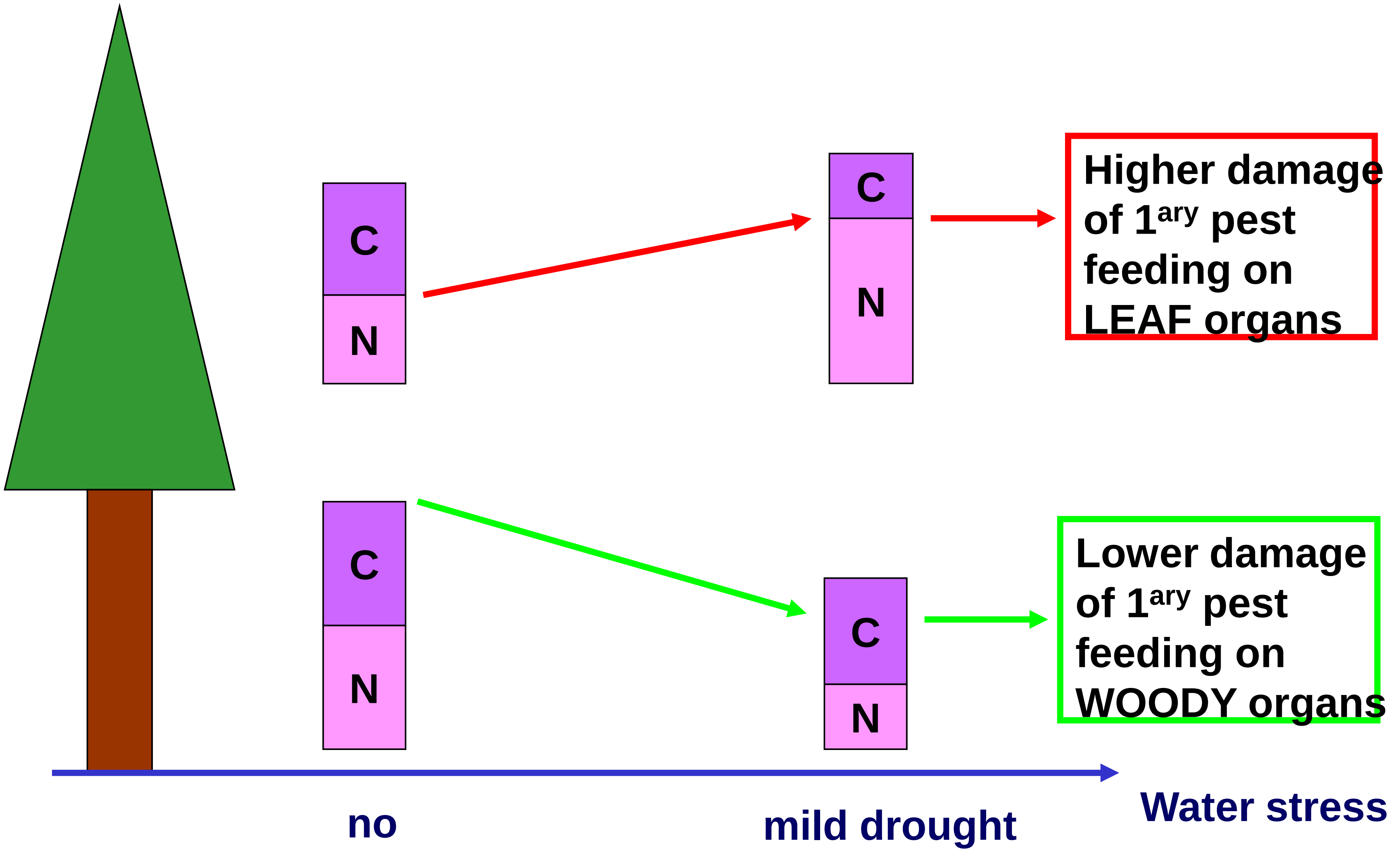
Response of secondary pest and disease to drought: the Growth - Differentiation Balance Hypothesis (GDBH)



Response of primary pest and disease to drought: the Plant Stress Hypothesis (C/N Hypothesis)

White 1969

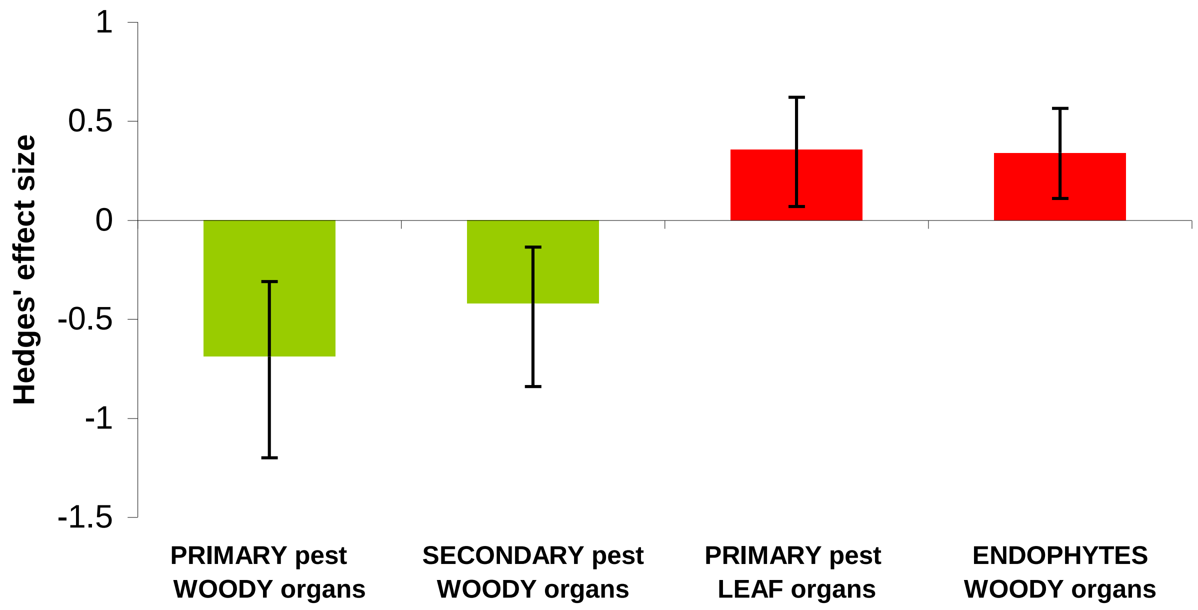
Water stress → hydrolysis of proteins + N-rich osmoprotectants → flow of N to canopy



Risk rating will change with drought severity

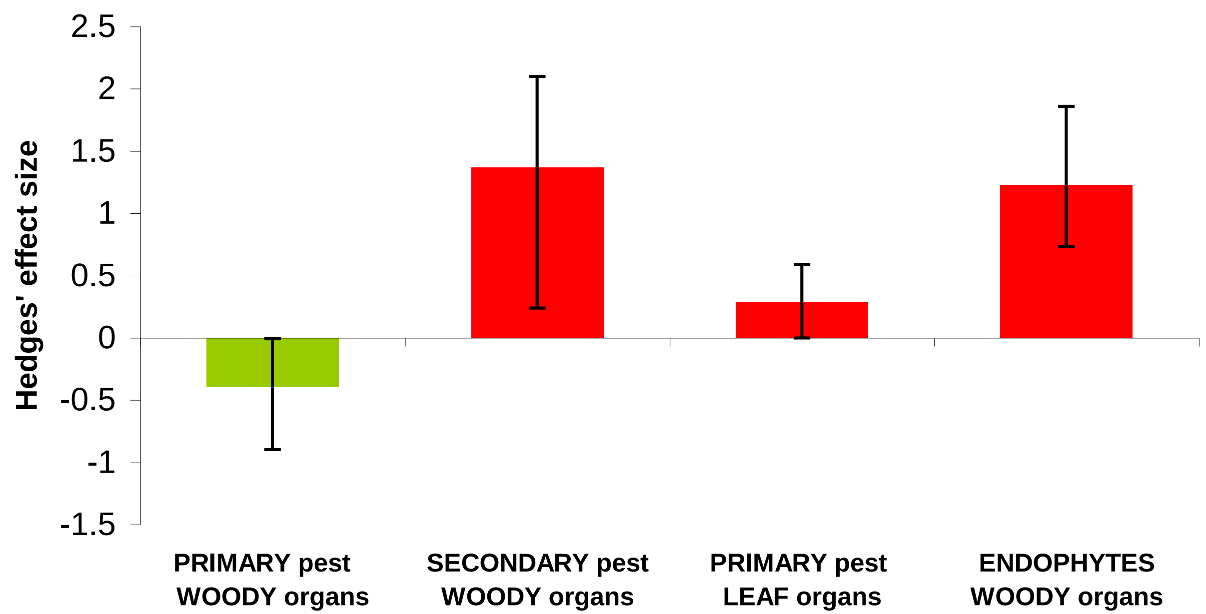
mild drought

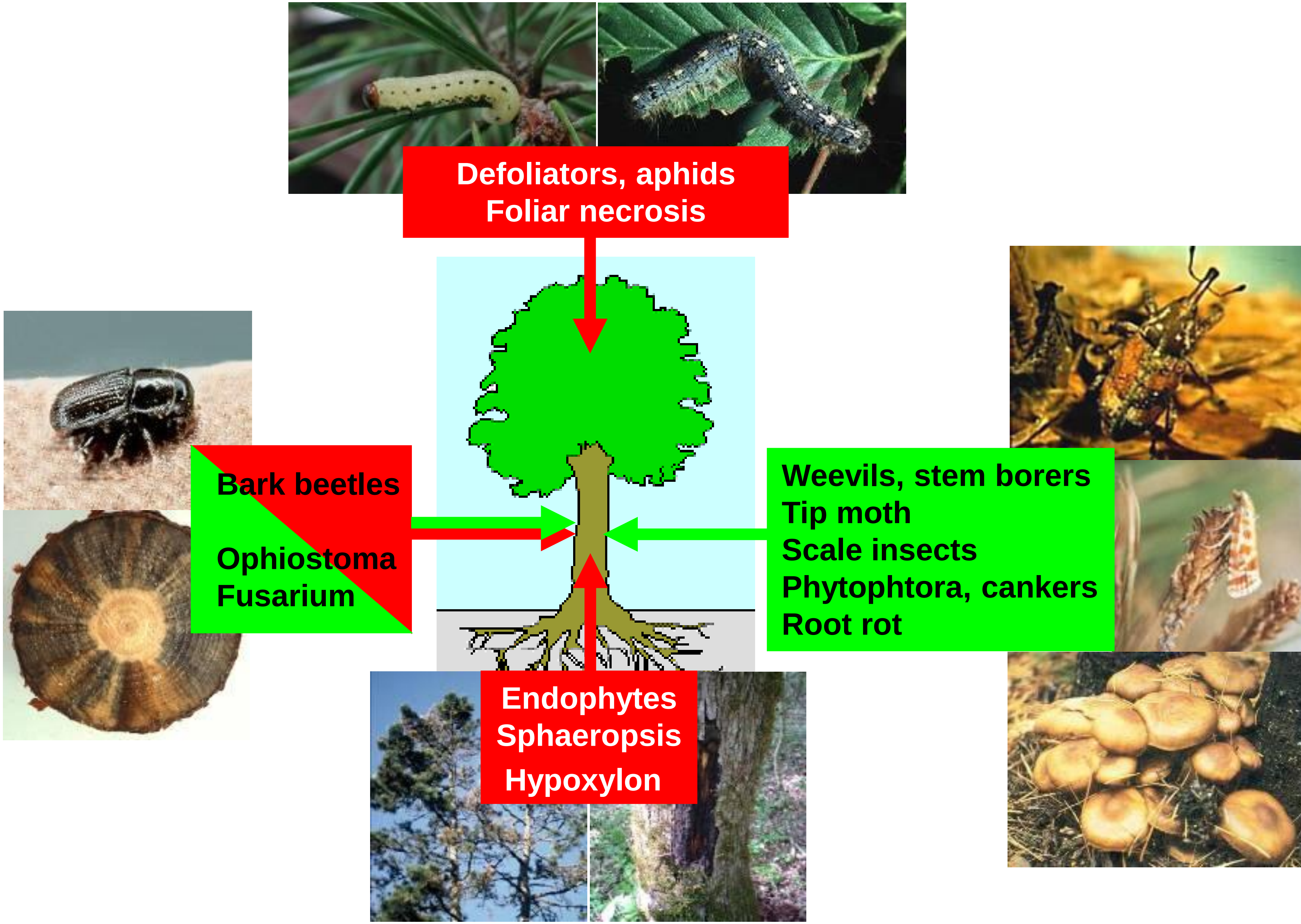
(PLS/PL50)<30%



severe drought

(PLS/PL50)>30%




Defoliators, aphids
Foliar necrosis
Bark beetles
Ophiostoma
Fusarium
Weevils, stem borers
Tip moth
Scale insects
Phytophtora, cankers
Root rot
Endophytes
Sphaeropsis
Hypoxylon