

# Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks

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**Abstract** – *Phoracantha semipunctata* (F.) larvae attack and kill trees in *Eucalyptus globulus* (Labill.) plantations in Mediterranean countries. To test the hypothesis that these attacks are more likely in arid environments, we examined the effects of water deficits in the host trees of *E. globulus* on the mortality and growth of *P. semipunctata* larvae. Trees subjected to water stress during two subsequent years were compared with rainfed and irrigated trees. Larvae of *P. semipunctata* were artificially introduced in the bark of trees of either treatment. Larvae mortality was lower and weight gain was higher in water stressed trees than on rainfed trees. There was no larvae survival in irrigated trees. These results were related to changes in moisture content and concentration of soluble sugars in the bark of the trees. The results of this study suggest that water stress had a major role on the survival and growth of the larvae.

**Cerambycidae / *Phoracantha semipunctata* / plant-insect interaction / water-deficit / bark borer**

**Résumé** – **Effets positifs de la sécheresse du sol sur la survie et la croissance des larves de *Phoracantha semipunctata* sur l'eucalyptus.** Le *Phoracantha semipunctata* (F.) (Coleoptera : Cerambycidae) est un ravageur commun des plantations d'*Eucalyptus globulus* (Labill.) des milieux méditerranéens, particulièrement dans les régions les plus arides. La mortalité et la croissance des larves de *P. semipunctata* ont été comparées in vivo sur des arbres d'*E. globulus* soumis à trois traitements : stress hydrique durant deux années consécutives, irrigation et témoins. Des larves de *P. semipunctata* ont été artificiellement introduites dans l'écorce des arbres soumis aux trois traitements. Une plus faible mortalité et une augmentation de la biomasse des larves ont été obtenues chez les arbres stressés, comparativement aux arbres témoins. Chez les arbres irrigués la mortalité de larves était totale. Les effets de la teneur en eau et de la concentration en sucres solubles de l'écorce sur la mortalité larvaire ont aussi été testés. Nos résultats permettent de conclure que le stress hydrique est un facteur déterminant dans la réussite de la colonisation de l'arbre par les larves de *P. semipunctata*.

**Cerambycidae / *Eucalyptus globulus* / *Phoracantha semipunctata* / interaction plante-insecte / contrainte hydrique**

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## 1. INTRODUCTION

*Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae), a phloem-boring insect, is a monophagous insect that has become a pest in several countries where eucalyptus has been planted as an exotic [5, 10, 39], including Portugal. During drought years, this exotic beetle attacks and kills a higher proportion of standing eucalyptus than in its native land in Australia [6, 12, 33]. Heavy infestations of *P. semipunctata* larvae result in destruction of the cambium layer and the rapid death of the tree [10, 13, 33]. *P. semipunctata* has no aggregation pheromones and no mutualistic fungi associated, which could augment its capacity to colonise living trees [28]. Females of *P. semipunctata* lay eggs in batches under loose bark or in bark crevices of *E. globulus* trees. After few days, eggs hatch and the neonate larvae bore through bark and feed mainly along the cambium, phloem and some recently differentiated xylem [7, 13]. Mature larvae bore into the sapwood to construct a pupal cell. Adult insects are present continuously from early spring through September [12]. Development from egg to adult requires 3 months in average but it can take from 2.5 to 12 months depending on the temperature. In Portugal, *P. semipunctata* can have one to two generations per year.

Several studies have linked outbreaks of bark beetles to the occurrence of drought conditions on coniferous plants [8, 11, 15, 17, 21, 35]. It has been suggested that plants subjected to abiotic stress may become more suitable as food for insects, due to increased nutritional quality (e.g. soluble nitrogen) and/or reduced concentrations of defensive chemicals [21, 30, 31, 41, 42]. However, the postulate that drought stress may cause insect outbreaks via direct effects on the host plants is still largely unresolved [19, 20], namely for angiosperm trees [18]. Discrepancies between stress experiments and field observations can be explained by the short duration of stress treatments because, in nature, outbreaks of bark borers often occur after several years of stressful conditions [18, 23]. Also, unnatural manipulation of mature trees aiming to induce water stress, e.g. root trenching, may cause confounding effects (e.g. changes in carbohydrate partitioning) and unclear insect responses [3, 25].

Resistance of eucalyptus to attack by *P. semipunctata* has been attributed to bark moisture [6, 12, 14] and/or kino exudation [4, 6, 33, 39, 40], a brown viscous fluid composed of polyphenols that develops in traumatic parenchyma after mechanical injury or insect damage to bark [34]. However, in these studies the authors used tree logs [6, 12], root trenched trees and young potted trees

that were subject to short periods of water stress [12, 14]. None of these studies used mature trees subjected to natural water stress and/or assessed the importance of nutritional quality of the bark of the trees to the *P. semipunctata* larvae.

This study aimed at testing the hypothesis that water deficits increase the susceptibility of eucalyptus trees to *P. semipunctata* attack. In this study, tree susceptibility [11] was assessed by the percentage of larvae survival and larvae growth. For this we induced water stress in mature eucalyptus trees without direct damages on trees (apart from incisions made to install larvae) or concomitant changes in their atmospheric environment to study the effect of water deficits on the susceptibility of trees to be colonised and eventually killed by *P. semipunctata*. We studied the influence of water stress on tree growth, bark moisture content, kino production, bark soluble sugars and total nitrogen concentration. Larvae response to bark physical and nutritional characteristics was assessed by measuring larvae survival and growth.

## 2. MATERIALS AND METHODS

### 2.1. Study site

The study was conducted in an 8-year-old stand of *Eucalyptus globulus* (Labill.) (first rotation), planted with a 3 × 3 spacing (1010 trees per ha) with almost no understory, at Herdade de Espirra (38°38' N–8°36' W). Average tree height was of 16.01 m and average diameter at breast height (*d.b.h.*) of 14.20 cm. Climate is of Mediterranean-type, with mean annual rainfall of ca. 600 mm, occurring mostly from November to March. Drought usually extends from the end of May to the end of September. Mean annual temperature is 16.3 °C. Soil is a Dystric Cambisol (FAO/UNESCO) 40-cm-deep overlying sandstone.

### 2.2. Experimental set-up

We randomly installed 6 plots of 144 m<sup>2</sup> on a homogeneous soil (6 soil profiles were analysed). Each plot included 16 trees. Each of the following treatments was applied to 2 plots: **Irrigation (I)**: plots were irrigated from June to September 1993 and 1994. Water was supplied through micro-sprinklers to avoid tree water stress. Water supply amounted to an average of 114 mm per month in 1993 and 195 mm in 1994; **Control (C)**:

rained plots. Total rainfall from January to October was 536.4 mm in 1993 and 443.1 mm in 1994; **Stress (S)**: rainfall water was prevented from infiltrating the soil from March to September 1993 and 1994. In these plots, ground was covered with a plastic roof 40 cm above the soil and stem flow was diverted from reaching the soil through tubing. This system was carefully supervised every week. Moreover, around each plot, a 70-cm deep ditch was dug and lined with a PVC sheath (0.8 mm thick) to prevent lateral water movements. The rainfall excluded from each plot amounted to 45.6% and 30.3% of total precipitation in 1993 and 1994, respectively.

The trees chosen for all the observations and for the artificial colonisation with larvae of *P. semipunctata* were the four central trees of each plot, thus ensuring homogeneity of treatment application. A net protected these trees, from ground level until 1.5 m of height, to prevent natural attack by the borer.

### 2.3. Insects

Colonisation of trees was performed with larvae of *P. semipunctata*. Eggs were not used because the only natural enemy present in Portugal that could influence the efficacy of *P. semipunctata* colonisation is an egg parasitoid (*Avettianela* sp.). Eggs of *P. semipunctata* were collected in the field and reared in the laboratory as described in Hanks et al. [12] until eggs hatched. At the beginning of September 1994, first instars of the larvae were equally distributed into two incisions made in the bark of the four central trees of each plot (2 plots  $\times$  4 trees  $\times$  3 treatments). 20 larvae were introduced in half of the trees of all treatments and 15 larvae were introduced in the other half. Further, 15 larvae were introduced in each of 8 **logs (L)** from 4 trees cut two days earlier. Natural colonisation of trees was excluded by using a plastic net around trunks from ground until 1.5 m of height.

### 2.4. Tree water status

Pre-dawn leaf water potential ( $\Psi$ ) was measured in three leaves of each tree using a Scholander pressure chamber (P.M.S. 1000 Instrument, Corvallis, Oregon, USA). Trees were accessed with scaffolding, as the average height of the base of the crown was 12 m. Measurements were made in March, June, July and September 1994.

### 2.5. Tree growth

Tree diameter at breast height (*d.b.h.*) was measured at the end of each growing season to assess the effect of each treatment on tree growth. Total leaf area was determined in November 1994 by destructive sampling of all trees. The crown of each tree was divided in thirds and all leaves of each of these parts were collected into plastic bags that were immediately closed and weighted. From each third sub-samples were taken to estimate ratios of dry: fresh weight and surface area: dry weight. Dry weight was measured after leaves were dried at 80 °C, during 48 hours. The surface area was measured with an area meter recorder (Portable area meter, LI-3000). Total leaf area was calculated using these ratios and the total fresh weight of the thirds of the crown for each tree.

### 2.6. Bark moisture, soluble sugars and nitrogen content

Bark was sampled from the outer bark to the cambium using a 1.6 cm diameter cork borer. All bark samples were collected at dawn and approximately at breast height (1.30 m) in all trees, in June, July and September 1994.

Bark moisture content was determined in two samples per tree placed in hermetically closed boxes. These samples were weighted and dried at 80 °C. Bark moisture content of the logs was also determined in September. Soluble sugars concentration in the bark tissues was determined as described by Stitt et al. [37] and Stitt et al. [38] in samples that were frozen in liquid nitrogen immediately after collection. In the laboratory these samples were stored at -80 °C until analysed. Nitrogen concentration in the bark was determined by Kjeldhal method (Digestion System 40, kjeltec Auto Analyzer 1030). Bark samples were dried at 80 °C and ground to the consistency of a fine homogeneous powder.

### 2.7. Evaluation of insect attack

In November 1994 all trees were felled and bark was carefully removed to evaluate larvae mortality and larvae weight. The same methodology was used for logs (**L**).

### 2.8. Kino production

In November 1994, when all trees were felled and the bark removed, kino reaction due to the larval penetration was evaluated by drawing the exudation area of each

tree in a plastic sheet. These areas were measured with an area meter recorder (Portable area meter, LI-3000).

### 2.9. Statistical analysis

Multivariate repeated measurements analyses over time were performed for the following parameters: pre-dawn water potential ( $\Psi$ ), concentration of soluble sugars and total nitrogen of the bark using SAS (SAS Institute 1994). Within-subjects and between subjects effects were tested using Wilk's  $\Lambda$  and  $F$  tests, respectively. Multiple comparisons between pairs of the means of the treatments in each sampling date were performed using Duncan's multiple range test. Univariate analyses of variance (ANOVA) were used to assess differences among treatments for the relative increase in *d.b.h.*, leaf area and kino exudation area. Both for multivariate and univariate analyses of variance, the trees sampled in each plot were considered levels of a random factor nested within the levels of the treatment factor.

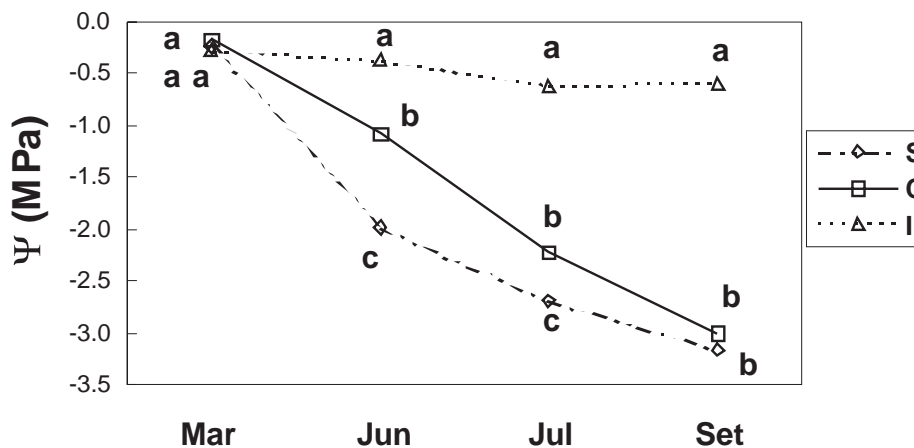
A stepwise logistic regression model was used to select the independent variables for a model of the mortality data of larvae introduced into incisions in the bark. A  $p$ -value of 0.05 for  $G$ , the likelihood ratio test statistic, was used both for entry and for remove. A polytomous independent variable with four categories (**S**, **I**, **C** and **L**) was considered. These categories were specified by three design variables setting all of them equal to zero for logs (**L**), the reference group. Larvae weight had neither a normal distribution nor homogeneous variances. Hence, we used a generalised linear model with a Gamma distribution function and a reciprocal link function.

### 3. RESULTS

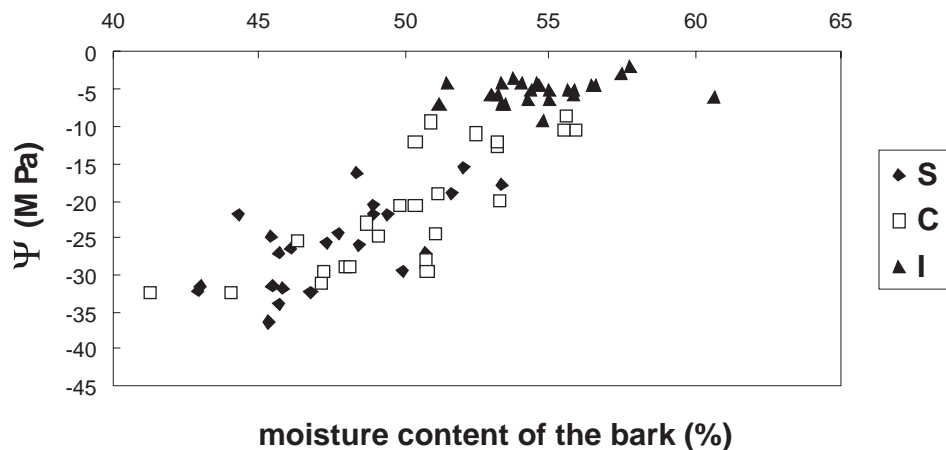
Values of pre-dawn water potentials were significantly affected by time (Wilk's  $\Lambda = 0.006928$ ;  $F_{3,9} = 430.01$ ;  $P < 0.001$ ) and by the time  $\times$  treatment interaction (Wilk's  $\Lambda = 0.0003978$ ;  $F_{6,14} = 114.67$ ;  $P < 0.001$ ). In March there were no significant differences in leaf water potential ( $\Psi$ ) between treatments as irrigation had not begun and rain exclusion roofs were just installed. At the beginning of summer, trees of treatment **S** had lower values of pre-dawn water potential ( $F_{2,9} = 161.50$  in June;  $F_{2,9} = 319.15$  in July;  $P < 0.001$  for both) than trees of treatments **C** and **I** (figure 1). In September, when larvae were introduced in the trees, pre-dawn water potentials ( $\Psi$ ) of trees of treatment **S** were significantly lower ( $F_{2,9} = 396.45$ ;  $P < 0.001$ ) than  $\Psi$  of trees of treatment **I** (figure 1). Even though **C** trees reached  $\Psi$  values almost as low as those of treatment **S** by the end of the summer, these lower values of water potential lasted for a much shorter period.

A significant linear relationship ( $R^2 = 0.75$ ;  $F_{1,70} = 215.67$ ;  $P < 0.001$ ) was found between bark moisture content and pre-dawn leaf water potentials ( $\Psi$ ) (figure 2). The bark moisture contents of the logs (**L**) and of **S** and **C** trees were significantly lower ( $F_{3,12} = 54.47$ ;  $P < 0.001$ ) those of **I** trees, at the time when larvae were introduced in the bark of trees (September). Logs (**L**) had the lowest bark moisture content ( $34 \pm 1.5\%$ ), followed by stressed (**S**,  $45 \pm 0.7\%$ ), control (**C**,  $47 \pm 1.1\%$ ) and irrigated (**I**,  $55 \pm 0.9\%$ ) trees.

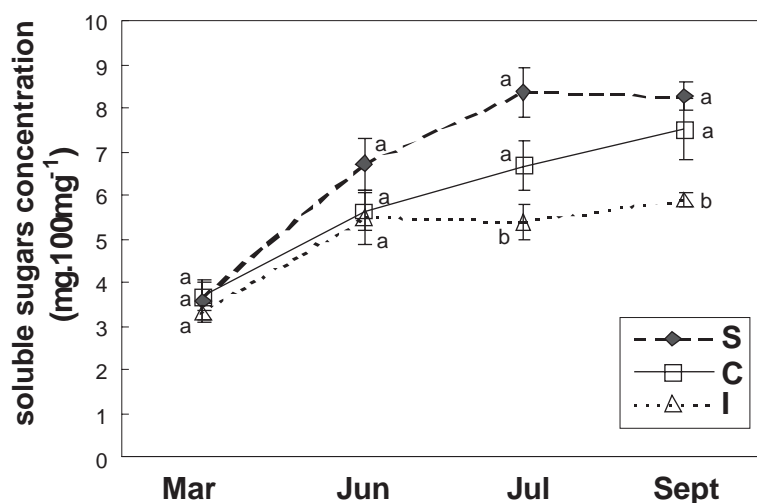
There was a significant reduction in total leaf area ( $31.8\%$ ;  $F_{2,9} = 10.96$ ;  $P < 0.01$ ) and in relative increase in



**Figure 1.** Pre-dawn leaf water potential ( $\Psi$ ) measured in March, June, July and September 1994. At each sample date, different letters mean significant differences at  $P = 0.05$  (Duncan's multiple test).



**Figure 2.** Relationship between pre-dawn leaf water potential ( $\Psi$ ) and bark moisture content. The relationship is significant at  $P < 0.0001$  ( $R^2 = 0.75$ ;  $F_{1,70} = 215.67$ ).



**Figure 3.** Concentration of soluble sugars in the bark ( $\text{mg } 100 \text{ mg}^{-1}$ ) measured in March, June, July and September 1994. At each sampling date, different letters mean significant differences at  $P = 0.05$  (Duncan's multiple test).

**Table I.** Total leaf area ( $\text{m}^2$ ) and relative increase in *d.b.h.* ( $\text{cm cm}^{-1}$ ) in the three treatments. Within each row, numbers followed by different letters are significantly different at  $P = 0.05$  (Duncan's multiple test). Values in brackets are standard deviations.

	S	C	I
Total leaf area	16.106 (3.799) <sup>a</sup>	35.779 (5.441) <sup>b</sup>	50.730 (7.252) <sup>b</sup>
Relative increase in <i>d.b.h.</i>	0.1069 (0.041) <sup>a</sup>	0.281 (0.068) <sup>b</sup>	0.278 (0.036) <sup>b</sup>

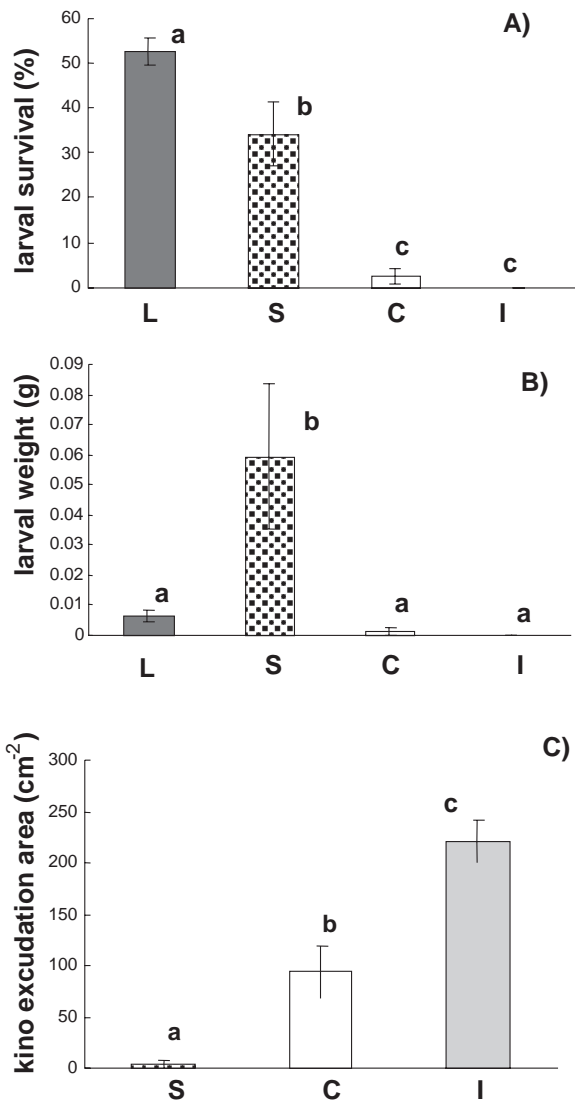
*d.b.h.* (38.47%,  $F_{2,9} = 4.41$ ;  $P < 0.05$ ) in trees of treatment **S** as compared to trees of treatment **I** (table I).

The concentration of soluble sugars (glucose, fructose and sucrose) in the bark was significantly different (Wilk's  $\Lambda = 0.047106$ ;  $F_{3,9} = 60.69$ ;  $P < 0.001$ ) with time (figure 3). In July and September, trees of treat-

ments **S** and **C** had higher concentration of soluble sugars in the bark (July:  $F_{2,9} = 6.38$ ;  $P < 0.05$ ; September:  $F_{2,9} = 7.68$ ;  $P < 0.05$ ) than trees of treatment **I** (figure 3). Concentration of total nitrogen in the bark was not significantly different between treatments ( $P > 0.05$ ; data not shown).

**Table II.** Logistic procedure. The value of the Pearson Chi-Square statistics for the model is 44.8597 ( $P < 0.0228$ ). Logs (L) are the reference group.

Variable	Parameter estimated	Standard error	Wald Chi-Square	$P >$ Chi-Square	Odds Ratio
intercept	-9.3614	2.6196	12.7704	0.0004	–
$\ln(b.m.c.)$	2.6348	0.7130	13.6566	0.0002	13.941
<b>C</b>	2.7670	0.5356	26.6902	0.0001	15.911
<b>I</b>	3.0348	0.7616	15.8777	0.0001	20.796



**Figure 4.** A) Larval survival in the three treatments: S, C, I and in logs (L). B) Larval weight in the three treatments: S, C, I and in the logs (L). C) Kino exudation area in the three treatments: S, C, I. In both graphs, different letters mean significant differences at  $P = 0.05$  (Duncan's multiple test).

The stepwise logistic regression model selected the logarithm of bark moisture content,  $\ln(b.m.c.)$ , as the covariate which explained larvae mortality in trees of treatment S. However, it does not totally explain larvae mortality in treatments C and I. The odds ratio (table II) for treatments C and I show an increase in the risk of larvae mortality, relatively to average value of the covariate and to treatment S (figure 4A). The generalised linear model adjusted to larvae weight shows that only the coefficient for treatment S is significantly different from zero ( $\chi^2 = 7.5782$ ;  $P = 0.0059$ ) (figure 4B).

Water deficits had a significant effect ( $F_{2,9} = 22.04$ ;  $P < 0.001$ ) in kino exudation area by trees. Trees of treatment S had the lowest kino exudation area and trees of treatment I the highest (figure 4C). Moreover, only 25% of the water stressed trees (S) had kino exudation, while 75% of control trees (C) and 88% of irrigated trees (I) had kino exudation.

#### 4. DISCUSSION

*E. globulus* trees subjected to rain exclusion (S) suffered severe water stress since the beginning of the summer onwards, reaching values of leaf water potentials close to the minimum of tolerance for this species [26]. Water deficits reduced tree growth and affected carbon metabolism, increasing the concentration of soluble sugars in the bark tissues. Similar results were found for other eucalyptus trees [24] and in several Mediterranean species [9, 22, 29].

The mortality of *P. semipunctata* larvae was lower in water stressed trees than in control and irrigated trees. Larvae mortality seemed to be related to bark moisture content, as neonate larvae boring through the bark can not survive in an environment saturated with water [6, 12, 14, 27, 39]. The highest larvae survival rate was found in logs that had the lowest bark moisture content. In this type of feeding guild, the close contact of larvae

with the tree tissues makes bark moisture content a critical factor for larvae survival. A small difference in bark moisture content between water stressed trees and control trees was reflected in much higher survival percentage of larvae in stressed trees. These results indicate the existence of a moisture content threshold [14] of near 45% above which larvae survival decreases.

Water deficits also affected kino exsudation. In water stressed trees there was almost no kino exsudation, whereas in irrigated trees there was an abundant exsudation as was described by some authors [6, 33]. Nevertheless, kino exsudation could not be the main factor explaining the reduced survival of larvae in irrigated trees. Between bark injury and kino exsudation there was a time lag [12] that could be of at least two weeks [16, 34] but signs of small larval galleries in irrigated trees indicated that larvae were dead in the first days of boring. This was supported by the observation that in some irrigated trees there was no kino exsudation and nonetheless there were no live larvae. Nevertheless, in some control trees where larvae were able to succeed against the initial tree defences, dead larvae covered with kino could be seen in galleries. When larvae growth was slow, kino production by trees might kill them.

Higher concentration of soluble sugars in the bark of water stressed trees could explain higher weight gains of larvae growing in these trees. Chararas [6] obtained faster larvae growth in an artificial environment rich in soluble sugar. Nitrogen can also be an important factor in larvae development [43, 44] but in our experiment total nitrogen in the bark was not affected by water stress. However, total nitrogen is probably not a good indicator of the nitrogen availability to insects [1, 32]. Soluble forms of nitrogen that can be more readily used by insects [2] can increase due to water stress [3, 36].

In this experiment it was shown that water stress could play an important role in the susceptibility of mature *E. globulus* trees to *P. semipunctata* attack. These results indicate that water stress effects on insect performance are non-linear [11, 18], as above a certain threshold of bark moisture content larvae survival and growth declined. Moreover, water stress seemed to positively affect larvae growth due to higher soluble sugar concentration in the bark of stressed trees than in well-watered trees. These results were independent from any direct damage to the trees or direct effect of abiotic conditions on the insect population. Understanding the relationship between water stress and susceptibility of trees to insect attack is of the most importance to forest management and decision-makers.

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## REFERENCES

- [1] Bernays E.A., Chamberlain D.J., Leather E.M., Tolerance of acridids to ingested condensed tannins, *J. Chem. Ecol.* 7 (1981) 247–256.
- [2] Bernays E.A., Chapman R.F., *Host-Plant Selection by Phytophagous Insects*, Chapman & Hall, New York, 1994.
- [3] Bultman T.L., Faeth S.H., Impact of irrigation and experimental drought stress on leaf-mining insects of Emory oak, *Oikos* 48 (1987) 5–10.
- [4] Bytinski-Salz H., Neumark S., The Eucalyptus borer (*Phoracantha semipunctata* F.) in Israel, *Trans. IXth Int. Congr. Ent.* 1 (1952) 696–699.
- [5] Cavalcaselle B., Osservazioni sulla diffusione di *Phoracantha semipunctata* F. in Sardegna, Sicilia e nell'Italia centro-meridionale, *Atti XII Congr. Naz. Ital. Entomol.* II (1980) 455–464.
- [6] Chararas C., Biologie et écologie de *Phoracantha semipunctata* F. (Coléoptère Cerambycidae xylophage) ravageur des eucalyptus en Tunisie, et méthodes de protection des peuplements, *Ann. Inst. Nat. Rech. For. Tunis* 2 (1969) 1–37.
- [7] Chararas C., Courtois J.E., Le Fay A., Thuillier A., Biologie, évolution et nutrition de *Phoracantha semipunctata* F. Coléoptère Cerambycidae spécifique des Eucalyptus, *Comptes-Rendus Séances Soc. Biol.* 165 (1971) 1565–1568.
- [8] Coulson R.N., Population dynamics of bark beetles, *Ann. Rev. Entomol.* 24 (1979) 417–447.
- [9] Diamantoglou S., Kull U., Kohlenhydratgehalte und osmotische Verhältnisse bei Blättern und Rinden von *Arbutus unedo* L. und *Arbutus andrachne* L. Jahresgang, *Ber. Deutsch. Bot. Ges. Bd.* 97 (1984) 433–441.
- [10] Drinkwater T.W., The present pest status of eucalyptus borer *Phoracantha* spp. in: South Africa, *Proc. I Congr. of the Entomological Society of Southern Africa*, 1975, pp. 119–129.
- [11] Guérard N., Dreyers E., Lieutier F., Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): Estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem, *Ann. For. Sci.* 57 (2000) 681–690.
- [12] Hanks L.M., Paine T.D., Millar J.G., Mechanisms of resistance in *Eucalyptus* against larvae of the eucalyptus longicorn borer (Coleoptera: Cerambycidae), *Environ. Entomol.* 20 (1991) 1583–1588.
- [13] Hanks L.M., Paine T.D., Millar J.G., Hom J.L., Variation among *Eucalyptus* species in resistance to eucalyptus borer

in Southern California, *Entomologia Experimentalis Applicata* 74 (1995) 185–194.

[14] Hanks L.M., Paine T.D., Millar J.G., Campbell C.D., Schuch U.K., Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae), *Oecologia* 119 (1999) 400–407.

[15] Heinrichs E.A., Global food production and plant stress, in: Heinrichs E.A. (Ed.), *Plant Stress-Insect Interactions*, John Wiley & Sons, New York, 1988.

[16] Hillis W.E., Ethylene and extraneous material formation in woody tissues, *Phytochem.* 14 (1975) 2559–2562.

[17] Jones C.G., Coleman J.S., Plant Stress and Insect Herbivory: Toward an Integrated Perspective, in: Mooney H.A., Wimmer W., Pell E.J., (Eds.), *Response of Plants to Multiple Stresses*, Academic Press, London, 1991, pp. 249–280.

[18] Koricheva J., Larsson S., Haukioja E., Insect performance on experimentally stressed woody plants: a meta-analysis, *Annu. Rev. Entomol.* 43 (1998) 195–216.

[19] Larsson S., Stressful times for the plant stress–insect performance hypothesis, *Oikos* 56 (1989) 277–283.

[20] Lavallée R., Albert P.J., Mauffette Y., Influence of white pine watering regimes on feeding preferences of spring and fall adults of the white pine weevil *Pissodes strobi* (Peck), *J. Chem. Ecol.* 20 (1994) 831–845.

[21] Mattson W.J., Haack R.A., The role of drought stress in provoking outbreaks of phytophagous insects, in: Barbosa P., Schultz J.C., (Eds.), *Insect Outbreaks*, Academic Press, New York, 1987, pp. 365–407.

[22] Meleti-Christou M.S., Rhizopoulou S., Diamantoglou S., Seasonal changes of carbohydrates, lipids and nitrogen content in sun and shade leaves from four mediterranean evergreen sclerophylls, *Environ. Experiment. Bot.* 34 (1994) 129–140.

[23] Mopper S., Whitham T.G., The plant stress paradox: effects on pinyon sawfly sex ratios and fecundity, *Ecology* 73 (1992) 515–525.

[24] Myers B.A., Neales T.F., Osmotic adjustment, induced by drought, in seedlings of three Eucalyptus species, *Aust. J. Plant Physiol.* 13 (1986) 597–603.

[25] Myers B.J., Water stress integral – A link between short-term stress and long term-stress growth, *Tree Physiol.* 4 (1988) 315–323.

[26] Pereira J.S., Tenhunen J.D., Lange O., Beyschlag W., Meyers A., David M.M., Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal, *Can. J. For. Res.* 16 (1986) 177–184.

[27] Powell W., Age-specific life-table data for the Eucalyptus boring beetle, *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae), *Malawi. Bull. Ent. Res.* 72 (1982) 645–653.

[28] Raffa K.F., Berryman A.A., The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae), *Ecol. Monographs* 53 (1983) 27–49.

[29] Rhizopoulou S., Physiological responses of *Capparis spinosa* to drought, *J. Plant Physiol.* 136 (1990) 341–348.

[30] Rhoades D.F., Evolution of plant chemical defense against herbivores, in: Rosenthal G.A., Janzen D.H. (Eds.), *Herbivores: Their interaction with secondary plant metabolites*, Academic Press, New York, 1979, pp.1–55.

[31] Rhoades D.F., Offensive-defensive interactions between herbivores and plants: Their relevance in herbivore population dynamics and ecological theory, *Am. Naturalist* 125 (1985) 205–238.

[32] Scriber J.M., Slansky F.Jr., The nutritional ecology of immature insects, *Annu. Rev. Entomol.* 26 (1981) 183–211.

[33] Scriven G.T., Reeves E.L., Luck R.F., Beetle from Australia threatens eucalyptus, *California Agriculture* July–August (1986) 4–6.

[34] Skene D.S., The development of kino veins in *Eucalyptus obliqua* L'Hérit, *Aust. J. Bot.* 13 (1965) 367–78.

[35] Speight M.R., Wainhouse D., *Ecology and Management of Forest Insects*, Clarendon Press, Oxford, 1989.

[36] Stewart G.R., Larher F., Accumulation of Amino Acids and Related Compounds. Relation to Environmental Stress, in: Mifflin B.J. (Ed.), *The Biochemistry of Plants. AminoAcids and Derivatives*, Academic Press, New York, 1980, pp. 609–635.

[37] Stitt M., Bulpin P.V., Aprees T., Pathway of starch breakdown in photosynthetic tissues of *Pisum sativum*, *Biochim. Biophysic. Acta* 544 (1978) 200–214.

[38] Stitt M., Lilley R., Gerhardt R., Heldt H.W., Determination of metabolite levels in specific cells and subcellular compartments of leaves, *Methods in Enzymology* 174 (1989) 518–552.

[39] Tirado L.G., Lucha contra *Phoracantha semipunctata* Fab. en el Suroeste Español, *Bol. Serv. Plagas* 10 (1984)185–204.

[40] Tooke F.G.C., Insects injurious to forests and shade trees. *Plant Industry Series No 2, Bulletin 142*, Union of South Africa Department of Agriculture and Forestry, 1935, pp. 33–39.

[41] Waring R.H., Pitman G.B., Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack, *Ecology* 66 (1985) 889–897.

[42] White T.C.R., A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* New Zealand, *Oecologia* 16 (1974) 279–301.

[43] White T.C.R., The importance of a relative shortage of food in animal ecology, *Oecologia* 33 (1978) 71–86.

[44] White T.C.R., The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants, *Oecologia* 63 (1984) 90–105.