

& PAGE, W. W. (1975). Food  
iegatus (L.).—*Acrida* 4, 33-45.  
orphism in bracken in relation

in press). The seasonal changes  
ability. *Chem. Ecol.*  
iversities Press.

a.—*Trans. R. ent. Soc. Lond.*

tyledoneae: *Daphniphyllaceae*  
lag.

A. H., LEHMAN, P. S., OBIOHA,  
1972). A literature review and  
nia Crantz).—326 pp. Athens,

gatus (Linnaeus) from eastern

nd feeding habits of *Zonocerus*  
. *Soc. Am.* 58, 426-436.

. Olfaction and cyanide sensi-  
nd the silkworm *Bombyx mori*.

ava, *Manihot esculenta*, in the  
hopper, *Zonocerus variegatus*  
t, 417-430.

. host selection in the Mexican  
llidae).—*Ann. ent. Soc. Am.*

32 pp. Ottawa, International

va toxicity: proceedings of an  
wa, International Development

optera: Acridoidea) in Sierra

for acyanogenesis in cassava.

Verbreitung der Blausaure bei  
bindungen bei Parietales und  
1341-1355.

cerus variegatus (L.) (Orthop-

ires de *Zonocerus variegatus*  
ic. *Fr.* 32, 161-170.

breakdown of linamarin from

a, 1977

## Physiological reactions of *Pinus radiata* to attack by woodwasp, *Sirex noctilio* F. (Hymenoptera: Siricidae)

J. L. MADDEN \*

C.S.I.R.O. Division of Entomology, Stowell Avenue, Battery Point, Tasmania, 7000, Australia

### Abstract

Physiological studies of *Pinus radiata* damaged artificially and of others attacked by *Sirex noctilio* F. indicated that temporary disturbances of the normal physiology of the host trees produce potential breeding sites for the woodwasp. Different physiological processes within trees were monitored after treatment and attack; these included changes in translocation, transpiration, phloem respiration and osmotic and moisture content. The response of the *S. noctilio* to trees baited with phloem extracts or monoterpene solutions was investigated. The results of these studies, together with the published findings of other workers on the effects of insect secretions on trees and the resistance phenomenon, were interpreted into a general hypothesis of the interaction of the insect with the host tree. It was found that damage impaired translocation and enhanced transpiration and phloem respiration. These changes resulted in changes in tissue permeability and increased the rates of monoterpene and water vapour loss through the bark. The attraction of *S. noctilio* to trees was related to these changes, and the lowered osmotic status of the phloem favoured egg deposition. Drilling also was accompanied by the secretion of arthrospores of the symbiotic fungus *Amylostereum areolatum* and mucus, which inhibited translocation. High water tensions in stressed trees favoured fungus invasion, and low turgor resulting from the permeability changes minimised resinosis at oviposition sites. Successful establishment of the fungus, together with the effects of the mucus, resulted in tree death and the creation of a suitable milieu for *Sirex* development. The hypothesis proposes that the outcome of any attack is related to the duration and effects of the initial stressor on the tree and the tree's ability to moderate these effects. The response in the physiology of individual trees to stress affects the probability of attack while the resultant interaction between insect and tree determines the intensity of drilling, arthrospore and mucus load, and tree susceptibility or resistance to that attack.

### Introduction

The woodwasp, *Sirex noctilio* F., is capable of attacking and killing *Pinus radiata* (Gilbert & Miller, 1952; Jackson, 1955; Rawlings, 1948), and its phytotoxic effects have been attributed to the combined effects of a mucus, which characteristically

\* Present address: Faculty of Agricultural Science, University of Tasmania, Hobart, Tasmania, 7000, Australia.

inhibits translocation from the needles, and the symbiotic fungus, *Amylostereum areolatum*, which eventually invades the entire stem (Coutts, 1969a, 1969b). The tree is inoculated with both mucus and arthrospores through the ovipositor during drilling. Spradbery (1973), working with different genera and species of siricids and host-trees, concluded that *S. noctilio* was the only species of woodwasp the attack of which may lead to the killing of living trees and that *P. radiata* was particularly vulnerable.

Madden (1968, 1971) reported that the attraction of woodwasps to host-trees could be initiated by any one of a number of surgical treatments but that the period between treatment and attack varied with the treatment applied. Thus, scorched or felled trees were attacked within 24 h after treatment, whereas trees that were pruned of their lower branches and girdled below the remainder or polled by the removal of all branches were not attacked until some 10–12 days later.

This paper considers changes in host-tree physiology associated with treated trees and trees naturally attacked by *Sirex*. A hypothesis is proposed to explain the sequence of physiological events involved in host-tree susceptibility and resistance and observed changes in host-tree location and oviposition behaviour by the wasp.

### Methods and materials

The investigation included both laboratory and field experimentation. The methods used are set out under headings arranged with respect to the hypothesis proposed rather than chronologically. The results are presented in the same order. In some instances, where appropriate for better understanding of the findings, the specific methods are given in the Results section.

#### *Crown damage and Sirex attack*

*Field occurrence.*—Surveys were conducted in areas of natural regeneration of *Pinus radiata* at Pittwater and a 30-year-old plantation at Scottsdale, Tasmania. Trees, either in study plots (0.04 ha) or on transect lines, were examined individually, and the presence of visible damage was recorded. Damage consisted of broken crowns, limb rub or gross damage from felling operations.

*Crown class and Sirex attack.*—The relationship between the type of crown and susceptibility to damage, attack and survival was investigated. Crown class was defined by the leader:lateral ratio (Mogren, 1955), i.e. the relative length of the leader shoot divided by the average length of its associated laterals. In practice, a sighting board, fitted with an eyepiece at one end and a Perspex plate at the other, was centred on the leader-whorl junction and the relative lengths read from a concentric circular grid scribed on the plate. Measurements were made on 20 freshly attacked trees and, as controls, the nearest unattacked trees of comparable class were measured.

*Simulation of crown damage.*—Localised damage to the crown regions of 30 *radiata* pines, 10–15 m high, was effected by 12-gauge shot and in five trees by the hand removal of all buds.

#### *General stomatal response to damage*

Samples of needles were removed from test and control trees and immediately coated with an acetone-base lacquer. After drying, the needle or the impression of its surface was examined under a binocular microscope, and the proportion and degree of stomates open were obtained by direct count.

#### *Transpirational loss*

*Water tensions developed following treatment.*—The water deficit of needles was obtained by severing branchlets and determining their tensions in a Schollander-type pressure bomb (Schollander *et al.*, 1965).

*Dendro-*  
Fritts &  
and contro-  
dendromete  
treatments  
and after tr

*Water*  
severed bra  
changes in  
infusion te  
1.0 cm into  
dye (Eversh  
drawn into  
elements fo  
The distanc  
lesion was m

In a sec  
trees, and  
instances, G  
that had fo  
considered  
elements at

#### *Suppression*

*Starch a*  
transversely  
solution and  
subjectively

*Amino-ac*  
thawing, a  
(Drummond  
chromatogra  
and the resp  
Initially, chri  
and intensity

#### *Respiration*

The resp  
Warburg tec  
tissue was re  
and taken to  
tissue cut in  
manometer  
attached to  
equilibration  
following nu  
girdled, two  
isolated by c  
at 48-h inter  
Within-tree c  
trees, betwe  
non-isolated  
different heig  
days after init

(L 2395)

*Dendrography.*—Recording dendrographs were constructed in the manner of Fritts & Fritts (1955) from obsolete thermohydrograph units and attached to test and control trees. These units were supplemented by the attachment of standard gauge dendrometer plates to additional trees. Both types of units were installed before the treatments were initiated and the diurnal course of daily change in increment before and after treatment was followed.

*Water tension of xylem elements.*—General values of water tension existing in severed branchlets were obtained with the pressure bomb (see above) and comparative changes in the tension of water in the xylem elements were obtained by a dye infusion technique. A 15-mm diameter nail was driven to a depth of approximately 1.0 cm into the stem and the point of entry surrounded by a small volume of intense dye (Evershed recorder ink), which adhered to the nail-bark junction. The dye was drawn into the lesion as the nail was slowly withdrawn and penetrated the xylem elements for a distance that was considered to be proportional to the original tension. The distance infused by the dye into the outermost tracheids above and below the lesion was measured after a strip of bark had been removed.

In a second approach, ovigerous *Sirex* females were placed on stressed and control trees, and a sample of the oviposition lesions was examined 12 weeks later. In all instances, the attack was slight and sub-lethal. The length of the resinosis streak that had formed in response to the oviposition lesion was measured. Again, it was considered that the extent of resinosis reflected the tension existing in the xylem elements at the time of forced attack.

#### *Suppression and translocation*

*Starch accumulation.*—Needles from stressed and control trees were collected, cut transversely and the cut ends immersed in a standard  $I_2$ -KI solution, dried of excess solution and examined beneath a binocular microscope. The amount of starch was subjectively assessed in the manner described by Coutts (1968).

*Amino-acid and carbohydrate levels.*—Collected needles were frozen and, after thawing, the sap was expressed by pressure, collected in standard 2  $\mu$ l microcaps (Drummond Sc. Coy., Broomall, Pa., U.S.A.) and spotted on Whatman No. 1 chromatography paper. The solvent system employed was BuOH:HAc:H<sub>2</sub>O (4:1:5) and the respective compounds were detected with ninhydrin and ammoniacal AgNO<sub>3</sub>. Initially, chromatograms were compared on an Eel densitometer and later both spot size and intensity were compared with phenylalanine and glucose standards.

#### *Respiration*

The respiration of needles and xylem and bark tissues was determined by standard Warburg techniques (Umbreit *et al.*, 1957). In the bark studies, an 8-cm<sup>2</sup> segment of tissue was removed from internodal areas of uniform bark, transferred to stoppered vials and taken to the laboratory where the outer margins were removed and the remaining tissue cut into six equal size segments, which were then transferred to preweighed manometer flasks, three segments per flask. Flasks plus tissues were weighed, attached to the manometer and placed in a 27.0  $\pm$  1°C water bath for a 20-min equilibration period. The respiratory activity of the bark was determined for the following numbers of trees: five attacked by *Sirex*, two conditioned by *Sirex*, six girdled, two polled, four felled, and two trees in which 0.5-m<sup>2</sup> areas of bark were isolated by cincturing (Coutts & Dolezal, 1966b). Activities were usually measured at 48-h intervals and compared to the activity of paired, untreated control trees. Within-tree comparisons were made between pruned and unpruned sections of felled trees, between the tissues above and below a girdle and between isolated and non-isolated tissues in cinctured trees. The respiratory activity of the bark at different heights up to 15 m in two attacked and two control trees was assessed six days after initiation of attack.

(L 2395)

E

Individual needles were separated from the fascicle and placed intact into the flasks to record needle respiration and, for xylem, 1-cm<sup>3</sup> blocks were removed with a knife-edge chisel and split into six equal sized slivers.

#### *Bark characteristics*

*Moisture content, diffusion pressure deficit and osmotic pressure.*—These values were assessed by the method previously described (Madden, 1974; Slatyer & McIlroy\*, 1961).

*Amino acids and sugars.*—Samples of bark were collected, frozen and 2- $\mu$ l samples of sap taken following thawing. The samples were applied to chromatography paper as in amino-acid and carbohydrate determinations (see above).

*Amylase activity.*—The amylase activity of bark sap collected from trees at certain intervals following treatment was determined by the time required for 2  $\mu$ l of sap to decolourise a standard I<sub>2</sub>-KI starch solution at 18°C. The standard starch solution consisted of 0.5 ml of 1.0% starch, 0.5 ml phosphate buffer (pH 6.4) plus 4  $\mu$ l I<sub>2</sub>-KI solution.

*Morphology.*—Hand-cut sections, about 12–15  $\mu$ m thick, were prepared from tissues sampled previously and fixed in formalin-acetic. The sections were stained with either aniline blue, Sudan III or iodine for detection of protein, lipid and starch, respectively.

*Oil yield.*—A fixed area of bark was collected at 2–3-day intervals from felled trees, weighed, diced and placed with water in a 1.0-litre flask, which was then connected to a semi-micro-cohobation still. Subsamples of bark were taken for moisture content and respiration determinations. Distillation was carried out for one hour and the yield of oil recorded. The yield of resin acids, which appear as amorphous coalescences in the distillation flask on cooling, was also obtained from one test tree. Yields of oil per unit of bark above and below a girdle and rates of respiration were obtained over a 16-day period.

*Gross changes in the permeability of isolated tissues.*—Segments of bark tissue were removed from treated and control trees with a 1.0-cm diameter cork borer and transferred to distilled water. The time required for obvious discolouration, viz. browning, to occur was noted. Such changes are indicative of intra- and inter-cellular leakage (Sacher, 1959). A manometer method in which a negative pressure was established on one side of a disc of bark proved unsuitable for assessing bark permeability, although it was successful in assessing the permeability of xylem blocks.

*Oleoresin exudation pressure.*—The pressures of treated and control trees were determined by the use of Bordeaux type capillary tubes (Bordeaux & Schopmeyer, 1957). Each tube was 15 cm long and the 1.0 mm capillary bore sealed at one end with Araldite. The tubes were driven into a 2.0-cm deep hole drilled into the tree. Three tubes per tree were used, and the lengths of the air columns recorded at 09.00 h. This measurement, divided into the length of the original air column, gives an approximation of the pressure in atmospheres (Wolfe & Maple, 1965), and by conversion, pascals.

#### *Analysis of air adjacent to bark*

*Respiratory gases.*—Gas-tight containers were prepared from tin cans fitted with a flange to accommodate the curvature of stems. The containers were positioned on test and control trees on Plasticene or wet cellulose gaskets and held in position by strong rubber bands. Standard gas sample tubes, fitted with screw clamps, were (O<sub>2</sub>) was analysed every 48 h with a Haldane gas analyser. The same method was

\* Slatyer, R. O. & McIlroy, I. C. (1961). Practical microclimatology: with special reference to the water factor in soil-plant-atmosphere relationships.—Cyclostyled report prepared and reproduced by C.S.I.R.O. Australia for UNESCO, 290 pp.

O<sub>2</sub>) was analysed employed to detect

*Moisture loss* bark was measured specially adapted, which the salt was pressure changes onto the tree with salt was attached in weight were observed, intact stem sheeting, and the pump.

*Oviposition* into were exposed to cut into 0.5-m length of the individual was removed and each day. A control was also prepared

#### **Results**

The level of attack was 0.5%, and at least woodwasp attack. number of stems or abraded bark in these situations compared

TABLE I. Number of stems

The incidence of 4.9% for damaged

Table II also shows more prone to attack sampling of apparatus when examined on to be conservative

Trees with high rub and breakage unattacked trees (Table to the attack. Results 1.44). The stress in stomatal aperture

0<sub>2</sub>) was analysed every 48 h with a Haldane gas analyser. The same method was employed to detect monoterpenes, using a Pye Unicam G. C. unit.

*Moisture loss through the bark.*—The rate of water vapour release through the bark was measured by the change in weight of anhydrous CuSO<sub>4</sub> enclosed in a specially adapted, stoppered, 2-cm o.d. vial. Each vial was fitted with a tray upon which the salt was spread, and a rubber diaphragm. The diaphragm served to attenuate pressure changes occurring when the vials were attached to perforated lids sealed onto the tree with Araldite. In practice, the preweighed vial containing the anhydrous salt was attached to the tree for 1–4 h, removed, restoppered and reweighed. Changes in weight were obtained for felled, pruned, unpruned trees and girdled trees. In other tests, intact stems cleared of branches were encased in heavy-gauge polythene sheeting, and the air space was continually evacuated via dry-ice traps with a vacuum pump.

*Oviposition intensity and weight loss.*—Five billets of different moisture content were exposed to 20 *Sirex* females in the insectary and, after 24 h oviposition, were cut into 0.5-m lengths and the ends coated with mastic (Shell L). The surface areas of the individual billets were determined and at the end of the experiment, the bark was removed and drill intensity assessed. The billets were held at 30°C and weighed each day. A control series consisting of five billets that were not exposed to *Sirex* was also prepared in the same way.

### Results

The level of attack in the Pittwater regeneration in 1967–68 was approximately 0.5%, and at least 50% of the attacked trees were obviously damaged before woodwasp attack. The incidence of damage was greatest in areas with the greatest number of stems per unit area, where a large number of trees had broken branches or abraded bark in the crown region. There were twice as many trees attacked in these situations compared to trees with no obvious damage (Table I).

TABLE I. Number of damaged or 'undamaged' trees attacked by *Sirex* in areas of high and low stocking. Total census, about 20 000 trees (> 2.5 cm diameter)

Condition of tree	Density of stems	
	High	Low
Damaged	42	6
'Undamaged'	21	26

The incidence of attack in two stands of mature trees at Scottsdale was 21.0 and 4.9% for damaged and 11.2 and 5.6% for undamaged trees respectively (Table II).

Table II also shows that trees in the subdominant and suppressed classes were more prone to attack, irrespective of the presence or absence of damage. The sampling of apparently undamaged trees revealed that many were in fact damaged when examined on the ground so that the figures for damaged trees must be considered to be conservative estimates.

Trees with high leader-lateral ratios (L/1) were more prone to damage by limb rub and breakage, and attacked trees had, in general, higher L/1 values than unattacked trees (Table III). Within the attacked trees, approximately half succumbed to the attack. Resistant trees had higher L/1 values than susceptible trees (1.82 vs. 1.44). The stress imposed by felling, crown damage, etc., resulted in an increase in stomatal aperture (Table IV).

Table II also shows that trees in the subdominant and suppressed classes were to the presence and 'absence' of damage

	Class of tree								Overall % attacked
	Dominant		Codominant		Subdominant		Suppressed		
	No. of trees	% attacked	No. of trees	% attacked	No. of trees	% attacked	No. of trees	% attacked	
<i>Mt. Helen*</i>									
Damaged, attacked	0	}0	6	}18.2	5	}21.7	4	}50.0	21.0
Damaged, unattacked	8		27		18		4		
'Undamaged', attacked	7	}1.75	32	}5.6	68	}24.3	59	}26.1	11.2
'Undamaged', unattacked	393		542		212		167		
							Total attack:	11.62	
<i>Cuckoo Stands</i>									
Damaged, attacked	0	}0	0	}0	1	}25.0	2	}3.9	4.9
Damaged, unattacked	1		5		3		49		
'Undamaged', attacked	0	}0	0	}0	13	}15.5	18	}24.7	5.6
'Undamaged', unattacked	112		280		71		55		
							Total attack:	5.56	

\*The Mt. Helen plantation occupies an exposed site in comparison to the Cuckoo plantation, and in 1969 a severe windstorm resulted in a high incidence of stem breakage and damage. Thus a higher proportion of trees (4.6%) appeared damaged as opposed to  $\approx 1\%$  in the Cuckoo plantation.

TABLE III. The leader : lateral ratios of attacked and unattacked trees

	No. of trees sampled	L/1 values	Significance
Attacked	20	1.53 $\pm$ 0.15	
Nearest unattacked	20	1.24 $\pm$ 0.91	0.1 < P < 0.2

TABLE IV. Degree of stomatal opening in stressed, crown shot and control trees (4 trees/treatment; 4 needles/tree)

	Stomata:			
	Fully open	> $\frac{1}{2}$ open	< $\frac{1}{2}$ open	Closed
Stressed	25.4	65.5	7.9	1.2
Control	5.1	25.8	53.5	15.6

TABLE V. Average water tensions (pascals) of branches taken from a treated series and from untreated control trees. Values adjusted relative to a control value of  $1766.4 \times 10^3$  pascals

	1-5 days post treatment	10-14 days post treatment
Forced <i>Sirex</i> attack and naturally attacked trees	2292.2 $\times 10^3$	{ 1863.0 $\times 10^3$ ultimately resistant 2463.3 $\times 10^3$ ultimately susceptible
Crown damaged	2001.0 $\times 10^3$	1545.6 $\times 10^3$
Girdled	1966.5 $\times 10^3$	1338.6 $\times 10^3$
Felled	2622.0 $\times 10^3$	3450.0 $\times 10^3$
Control	1766.4 $\times 10^3$	1766.4 $\times 10^3$

When  
felled or  
bomb, gr  
period, a  
In the fo

Both c  
according  
similar pat  
Dendro  
damaged.  
changes in  
the amplit  
experience  
asynchrony

and suppressed classes were  
age

Dominant		Suppressed		Overall % attacked
% attacked	No. of trees	% attacked	No. of trees	
7	4	50.0	4	21.0
	4			
3	59	26.1	167	11.2
	167			
Total attack:				11.62
0	2	3.9	49	4.9
	49			
5	18	24.7	55	5.6
	55			
Total attack:				5.56

Cuckoo plantation, and in 1969 a  
age. Thus a higher proportion of  
tation.

and unattacked trees

L/1 values	Significance
1.53 ± 0.15	0.1 < P < 0.2
1.24 ± 0.91	

rown shot and control  
(tree)

Closed
1.2
15.6

es taken from a treated  
justed relative to a  
als

10-14 days post treatment
1863.0 × 10 <sup>3</sup> ultimately resistant
2463.3 × 10 <sup>3</sup> ultimately susceptible
1545.6 × 10 <sup>3</sup>
1338.6 × 10 <sup>3</sup>
3450.0 × 10 <sup>3</sup>
1766.4 × 10 <sup>3</sup>

When shoots were detached from the above trees, or trees which were girdled, felled or subjected to forced *Sirex* attack, and water tensions assessed by the pressure bomb, greater values were found in most treatments of stressed trees for an initial period, after which they declined to values less than the controls (Fig. 1 and Table V). In the latter trees, water tensions progressively increased.

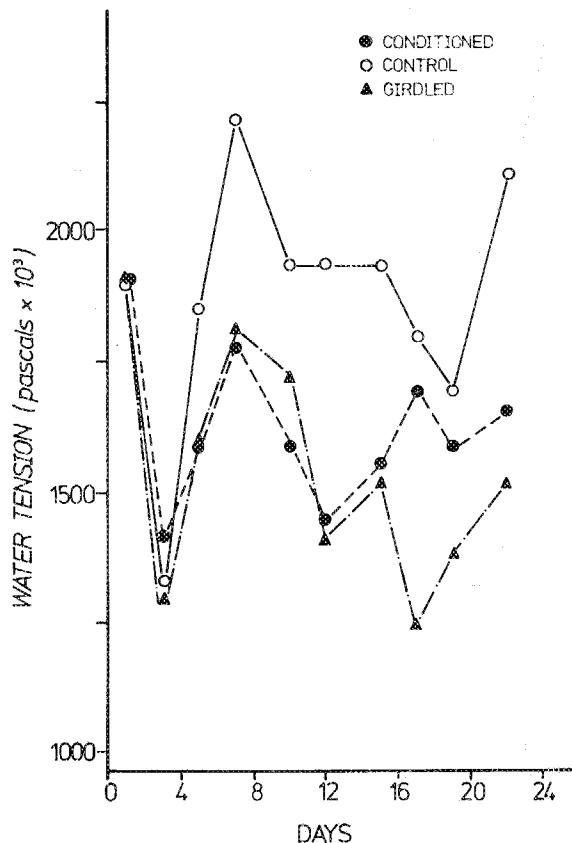


Fig. 1.—Changes in average water tension in needles of two sets of *P. radiata* trees (dbh 10–12 cm) untreated (control) or treated by either pruning and girdling at 3 m height or conditioned by caging 10 ovigerous *Sirex* females to the trunks at 0.5–1.5 m.

Both dendrographic patterns and respiratory trends gave characteristic patterns according to the various treatments which, though varying in their magnitude, had similar patterns irrespective of time of year.

Dendrographs revealed immediate reduction in diameter when trees were artificially damaged. This reduction was sustained for approximately 10 days, after which changes in diameter became synchronous with changes in the control trees, although the amplitude of the fluctuations was reduced. Similarly, trees that were debudded experienced a slight decrease in diameter and, in contrast to the controls, an asynchrony of diurnal diameter change occurred between days 10–18. The results

of the treatments on transpiration, as monitored by dendrography, are shown in Table VI and Fig. 2.

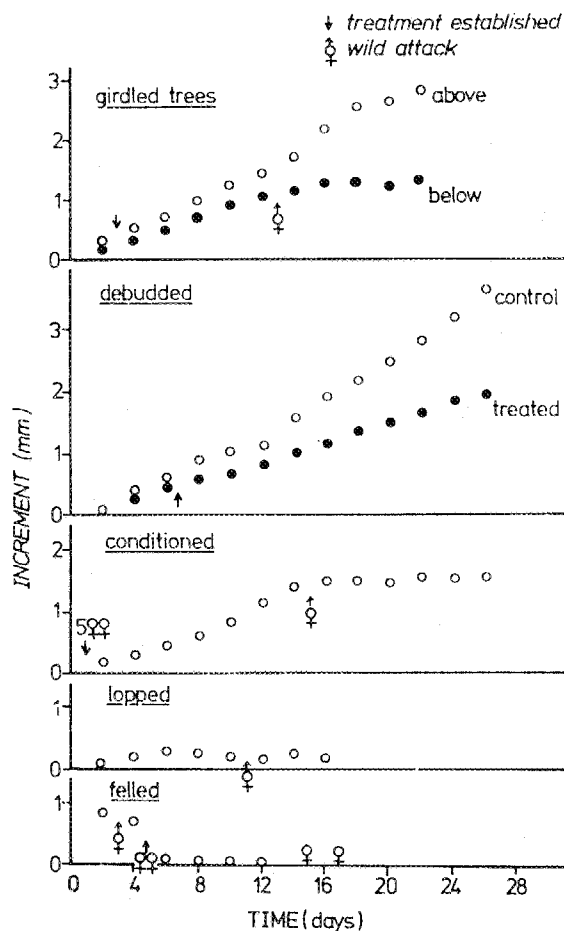


Fig. 2.—Average diurnal diameter increment associated with trees treated in different ways.

Dendrometer readings taken daily at 60-cm height intervals on two sets of three trees that were either lopped or girdled at 3.6 m revealed a nett expansion in comparison to untreated control trees measured at the same heights each day. However, the daily changes at each height in the two treatments varied in magnitude and direction. This variation was least in both treatments and in all trees at the 1.80-m level.

Trees that gave high pressure bomb readings, *i.e.* trees under high water tension, also had high rates of dye infusion. In 1969–70, many trees were defoliated by a geometrid, and the relationship between dye infusion/resinosis, degree of defoliation and water tension is shown in Fig. 3a, and between stressed (shot) and control trees at different heights above ground in Fig. 3b.

The degree of resinosis associated with the oviposition lesions in four stressed

Crown  
 Debudded  
 Polled  
 Girdled (below)  
 Girdled (above)  
 Felled  
 Forced attack  
 Sirex m injection  
 Natural

Average length of resinosis (mm)

Fig of the to les



TABLE VI. Changes in dendrograph patterns recorded on treated trees. Changes expressed relative to the control trees' diurnal performance

Treatment	Nos. of trees	Change noted as days post-treatment/observation	Direction of change	Duration of change	Remarks
Crown damage	4	Immediate	Shrinkage	Max. at day 10	Recovery by day 18
Debudded	3	12-14	Reduction and asynchrony	8 days	Restoration of normal pattern
Polled	6	Immediate	Amplitude reduced - movement ceases at 10-14 days	Gradual expansion	Tissue becomes inactive in expanded condition
Girdled (below girdle)	9	10-14	Reduction	Progressive shrinkage	
Girdled (above girdle)			Increase	Fate dependent on sustained root function via grafting	
Felled	2	Immediate	Progressive reduction	Maximum shrinkage by days 8-12	Irreversible
Forced <i>Sirex</i> attack (non-lethal)	4	10-12	Reduction	Recovery by days 18-20	
<i>Sirex</i> mucus injection	2	10-12	Reduction	Recovery by days 18-20	
Natural <i>Sirex</i> attack	5	8-14	Reduction	Dependent on susceptibility	

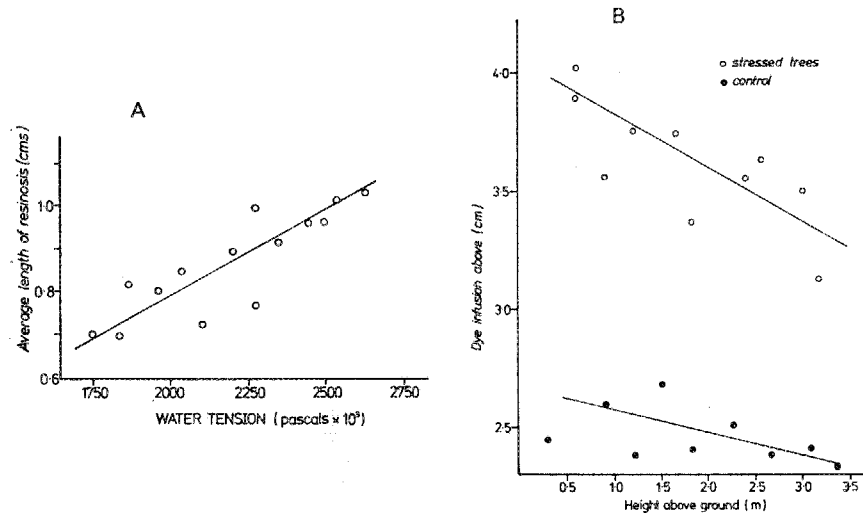


Fig. 3 (A)—Average water tensions of foliage of *P. radiata* trees recorded at the time of forced *Sirex* attack (5 ♀ /tree) and the resultant length of resinosis associated with the drilling lesions measured 12 weeks later. Water tension was directly proportional to the degree of geometrid defoliation. (B)—Extent of dye infusion into artificial lesions made at different heights in five stressed (crown damage by shooting) and five control trees.

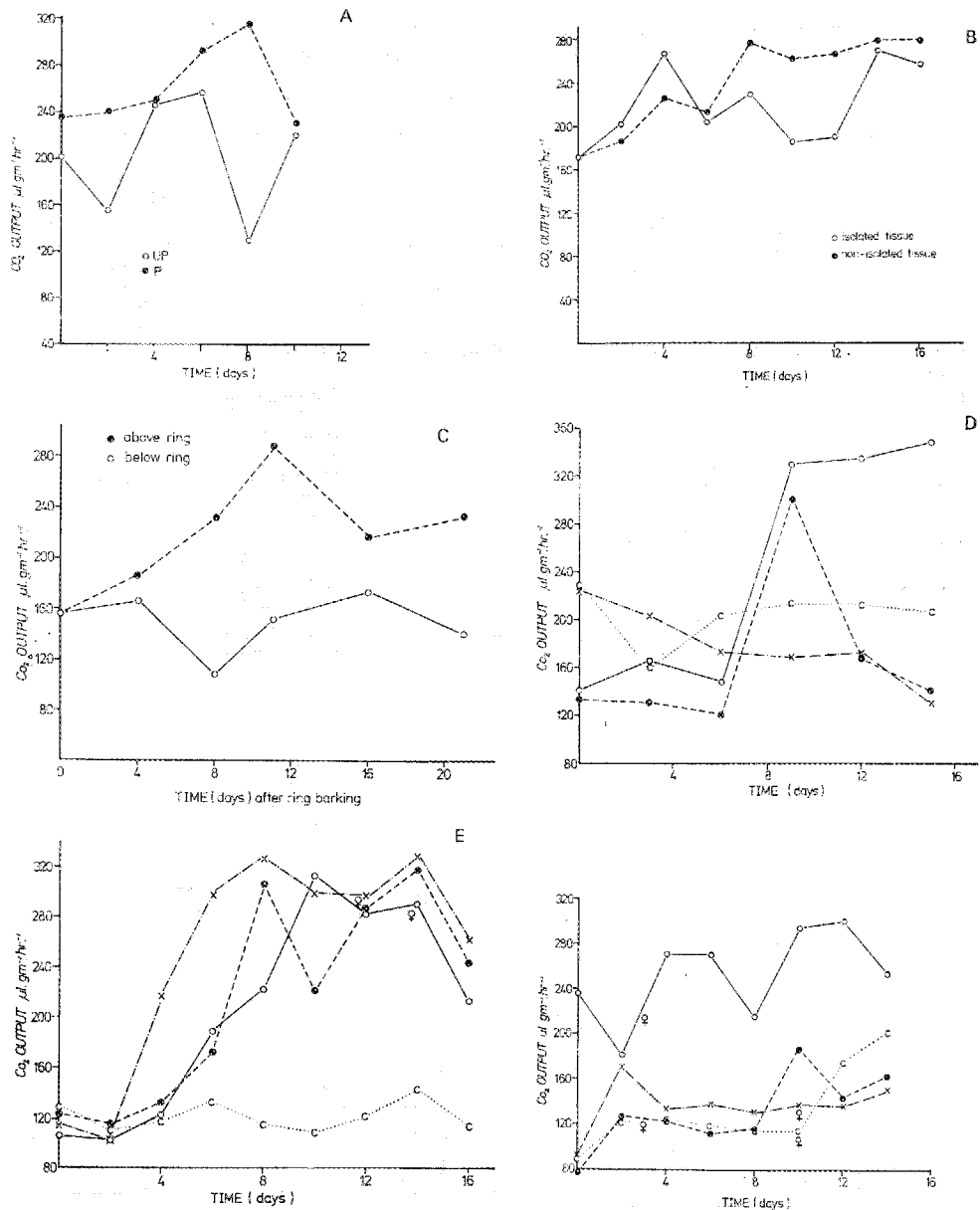
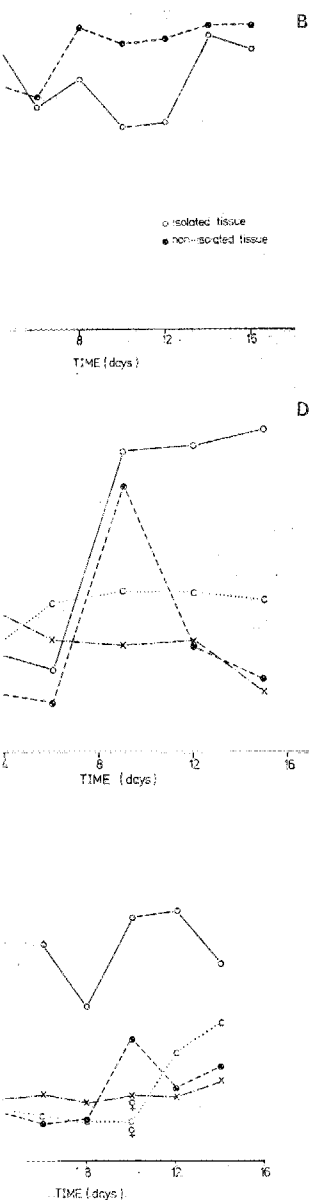


Fig. 4 (A)—Respiratory trends in the bark of 2-m long *P. radiata* billets that were either unpruned (UP) or pruned (P) of branches at the time of felling. (B)—Respiration of *P. radiata* bark tissue that was either left intact or isolated from translocation by cincturing, February 1968. (C)—Respiration above (●) and below (○) ring of bark tissue of a *P. radiata* tree that was pruned to a height of 3.5 m and ring-barked at 3.0 m, January 1967. (D)—Respiration of *P. radiata* bark tissue in a control tree (C) and in trees polled (×) and girdled above (○) and below (●) ring, March 1967. (E)—Respiration of *P. radiata* bark tissue in a control tree (C) and in three trees conditioned by caging five ovigerous *Sirex* females on their trunks on day 0, February 1967. (F)—Respiration of *P. radiata* bark tissue in a control tree that was attacked by one wild female on day 3 and received sustained attack from day 10 (C); in an unattacked control tree (●); in a polled tree (×) and in a naturally attacked tree where the attack was not less than 48 h old (○).

(shot) stressed and for All the star followed cells were those of were in Fong & Coin acids, the patterns and con following trees, an attractive with ma perform Height the resp



(B)—Respiration that were either cinctured or naturally attacked from day 10 (C); naturally attacked tree where (D).

(shot) and four control trees subjected to forced *Sirex* attack was greater in the stressed trees. The length of the resinosis streaks for stressed trees was  $2.65 \pm 0.31$  cm, and for the control trees  $1.06 \pm 0.25$  ( $P > 0.01$ ).

All treatments, with the exception of felled trees, resulted in initial increases in the starch content of needles to a maximum from 10–16 days after treatment followed by a decline. At the time of maximum concentration, all the mesophyll cells were packed with starch grains. The levels of free carbohydrate declined and those of amino acids increased in needle sap following treatment. These changes were indicative of impaired translocation from the needles (see Coutts, 1968, 1969b; Fong & Crowden, 1973).

Coincident with the changes in starch levels and soluble carbohydrate and amino acids, the respiration of needles and xylem and bark tissue followed characteristic patterns. All treatments resulted in increases in respiratory rates. In girdled, polled and conditioned trees, the onset of wild attack coincided with a decline in rate following a maximum rate achieved some  $10 \pm 1$  days after treatment. In felled trees, although wild attack commenced less than 24 h after felling, maximum attractiveness, i.e. the greatest number of females per tree per day, again coincided with maximum respiratory rates some 4–7 days after felling. The average respiratory performance of the treatments is shown in Fig. 4a–f.

Height and diameter of individual trees are positively correlated (Gray, 1944), and the respiratory rates of trees of different sizes varied widely. The respiration of the

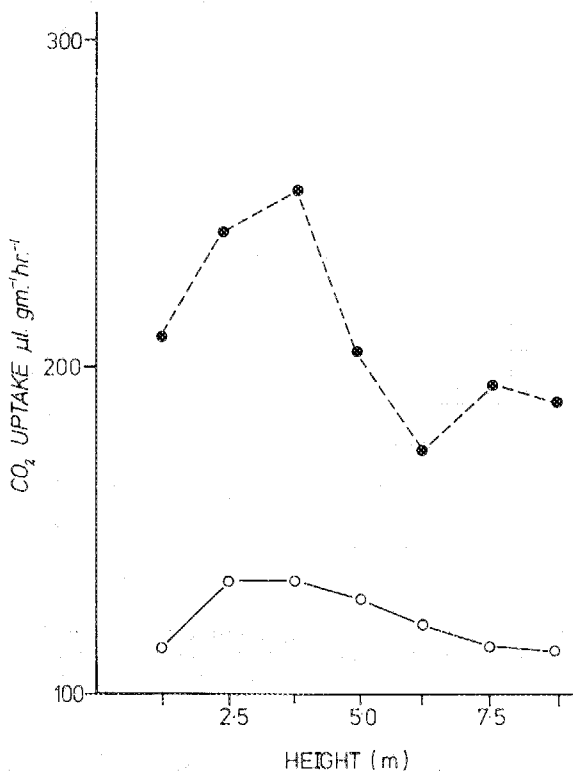


Fig. 5.—Respiration of *P. radiata* bark tissue at different heights in two control trees (○) and in two trees attacked seven days previously (●).

bark at different heights in the same tree also varied, and it was found that rates increased to a maximum at a height (which was related to diameter or tree size), and then declined; e.g. in control and attacked trees of 15 cm diameter at breast height, maximum rates occurred in the region of 2.5-4.0 m from the ground (Fig. 5).

Changes in moisture content and diffusion pressure deficit values are shown in Fig. 6 and, with the exception of felled trees, changes in these values in treated trees did not deviate significantly from those of the controls.

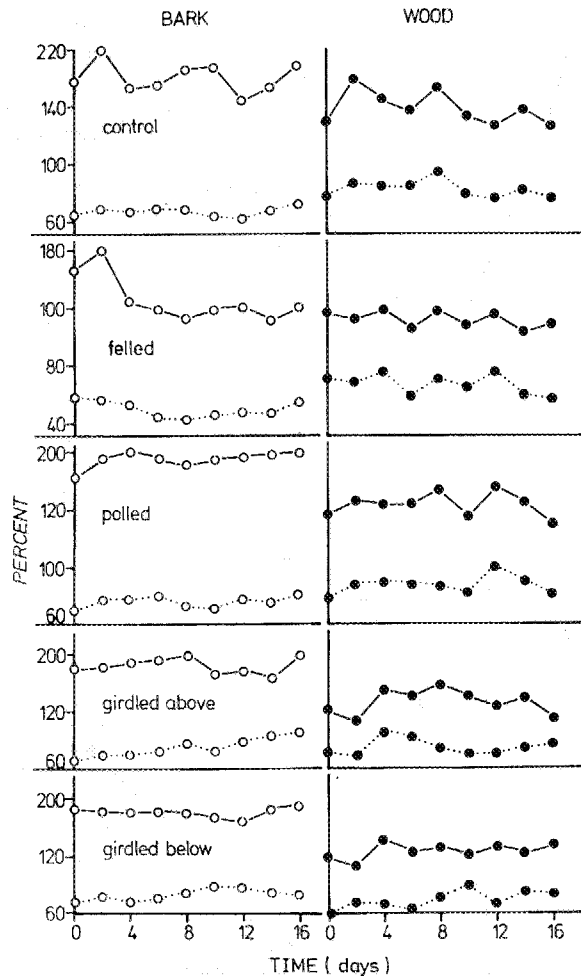


Fig. 6.—Changes in percentage moisture content (solid line) and percentage saturation (dotted line) in the bark and wood of *P. radiata* trees treated in different ways.

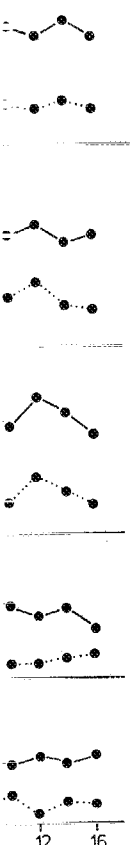
Osmotic pressures, on the other hand, did vary. Gradients from high to lower values were found with distance from the crown and from the top to the bottom of an internode. Osmotic pressure did not remain constant around the stem at a given height but varied widely, depending on the location of the sample site with

respect  
pressure  
trees wa  
in the b  
the onset

Levels  
all treat  
carbohydr  
isolating  
from these  
pads. Ch  
shown in  
Amyla  
desiccation  
had little  
shown in  
the delictio

and it was found that rates to diameter or tree size), 15 cm diameter at breast from the ground (Fig. 5). Deficit values are shown in in these values in treated

respect to branches at the node above. All treatments resulted in a lowering of pressure in time (Fig. 7). A consistent feature of the osmotic pressure of girdled trees was the transient but marked reduction in pressure that occurred on days 8-11 in the bark taken from above the girdle. This change in pressure coincided with the onset of diameter increase (Fig. 2).



ent (solid line) the bark and nt ways.

adients from high to lower om the top to the bottom tant around the stem at a on of the sample site with

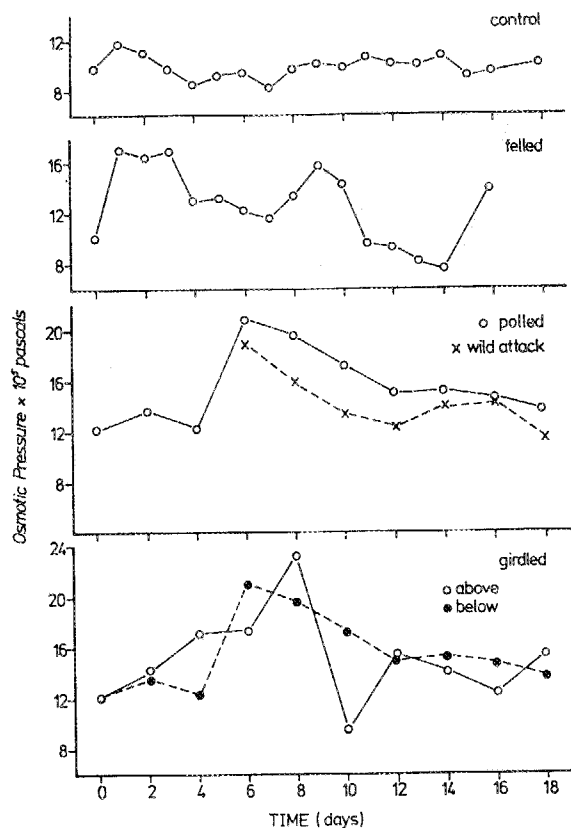


Fig. 7.—Changes in the osmotic pressure of bark sap in a series of treated *P. radiata* trees.

Levels of carbohydrate in the bark declined and amino acids increased following all treatments, and in felled trees it was shown that there was a movement of carbohydrate from the xylem into the bark. This movement was demonstrated by isolating some areas of bark from the xylem with aluminium foil. Excessive desiccation from these isolated tissues was prevented by covering the areas with wet cotton wool pads. Changes in carbohydrates and amino acids associated with treatments are shown in Fig. 8.

Amylase activity was enhanced initially after treatment but was impaired as desiccation progressed. Thus many defoliated trees and trees 2-3 weeks after felling had little or no activity. Relative activities of treated and control trees are shown in Table VII. The average time was reduced to approximately 1 min with the deletion of the felled tree samples.

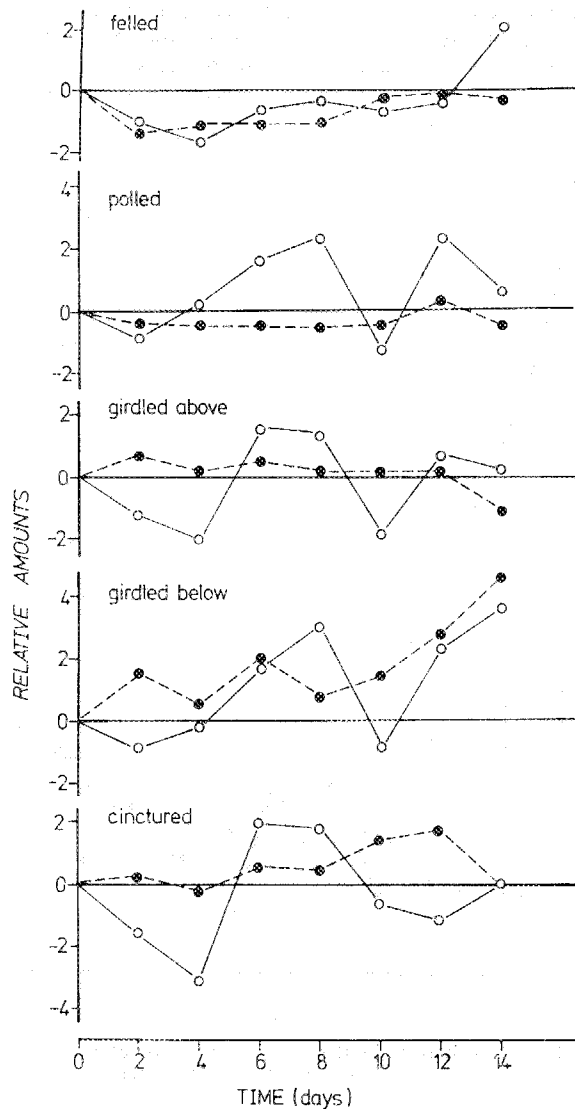


Fig. 8.—Changes in amounts of carbohydrate (○) and amino acids (●) in a series of treated *P. radiata* trees. Changes expressed in relation to control trees values.

TABLE VII. Time (min) required for a standard starch- $I_2$ -KI solution to be decolourised following the addition of 2  $\mu$ l of bark sap taken from trees just prior to test (about 15 min)

Treatment	n	Time to decolourise (min)
Felled, polled, girdled (below girdle), <i>Sirex</i> attacked and conditioned trees at 16-24 days after treatment	25	$1.50 \pm 0.36$
Control	8	$3.80 \pm 0.13$

Sections prepared from the bark of treated trees differed markedly from the appearance of sections prepared from healthy trees. There were marked changes in the shape of the cells and the number of starch granules present. In the treated trees, the outermost peripheral cells were characteristically flattened and angular, with little or no starch after 12-16 days. In addition, many of the cells contained large globules, presumably of resin acids. The sections from above and below a girdle 16 days after treatment are compared in Fig. 9.

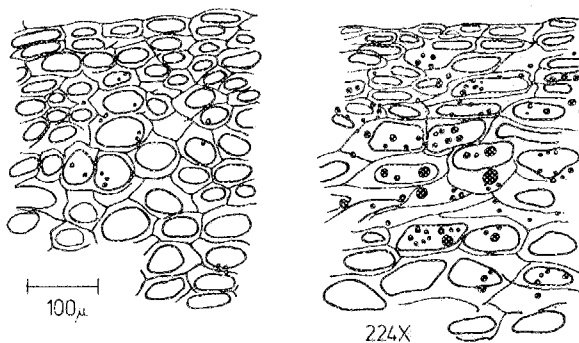


Fig. 9.—Diagrams of hand sections of bark tissue removed from above (left) and below (right) a girdle 16 days after the ring of tissue was removed. Note collapsed appearance and deposition of presumably resin acids in tissue from below the girdle.

The yield of steam-volatile oils per unit area of bark declined in time in felled trees, and this trend followed the decline in moisture content. Tissue respiration increased over the same period, and there was an increase in the yield of resin acids (Fig. 10).

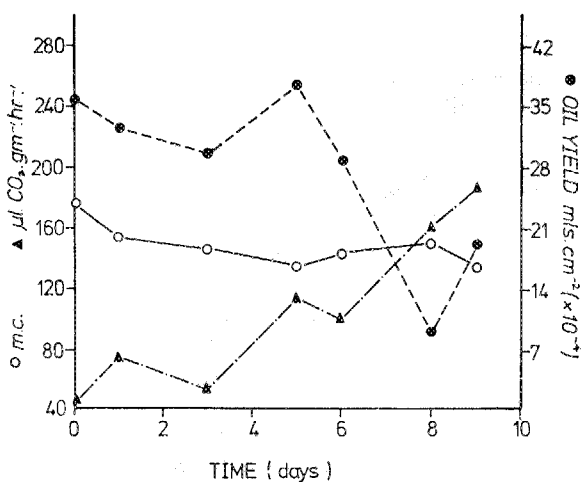


Fig. 10.—Changes in respiration (▲), oil yield (●) and moisture content (○) of bark removed from below the girdle on a series of 20 trees girdled on day 0.

...te (○) and  
...diata trees.  
...s values.

...-I<sub>2</sub>-KI solution to be  
...k sap taken from  
...n)

Time to decolourise (min)

1.50 ± 0.36  
3.80 ± 0.13

Oil yield from areas of bark removed above and below a girdle every two days indicated no real change in yield until the respiratory rate of the bark from below the girdle declined. Oil yield then declined as this tissue became progressively desiccated (Fig. 11).

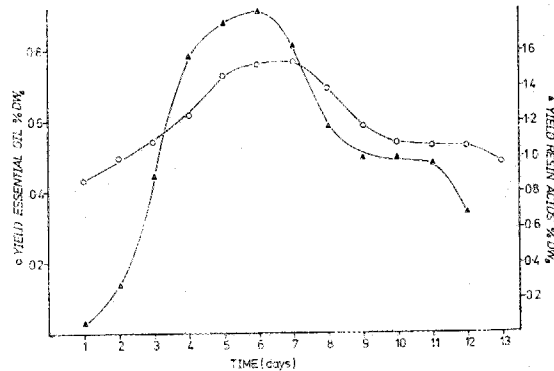


Fig. 11.—Steam-volatile oil and resin acid yield from areas of bark removed daily from three felled *P. radiata* trees.

When segments of bark were removed from treated and untreated trees and placed in distilled water or held in a water-saturated atmosphere, it was found that the tissues from treated trees discoloured at significantly greater rates than those from the control trees (Table VIII).

A notable feature in the sections of treated and attacked trees was the extensive brownening which occurred in the medullary rays.

Oleoresin exudation pressures are dependent on the turgor of the cells surrounding the resin ducts. There was a very rapid fall in the pressure in felled trees due to the rapid decline in overall turgor of the system. Girdled trees retained their pressure

TABLE VIII. Time required (min) for inner surface of bark discs to become brown when exposed in water-saturated air ( $n = 12$  for each treatment)

Treatment	Time to become brown (min)
<i>Sirex</i> attacked	$13.5 \pm 1.73$
Girdled tree (below ring at 20 days)	$11.5 \pm 0.96$
Control (unattacked)	$32.0 \pm 2.31$

TABLE IX. Changes in oleoresin exudation pressure associated with different treatments

Treatment	Oleoresin exudation pressure	Comments
Felled	$1 \times 10^5$ pascals	Very rapid fall in pressure.
Defoliated	$1 \times 10^5$ pascals	Progressive decline over 2–3 weeks.
Polled	$1 \times 10^5$ pascals	Progressive decline over 2–3 weeks.
Girdled	'normal' ( $4-6 \times 10^5$ pascals)	Rapid decline following attack. Gradual decline with physiological exhaustion.
<i>Sirex</i> attack	subnormal ( $1 \times 10^5$ pascals)	Dependent on tree's reaction to attack.

within  
howev  
physic  
deple  
transp  
Ch  
the in  
and b  
treatm  
These

No  
monote  
water w  
the free  
hexane,  
and 0.3  
trees in  
The  
rate th  
was ach  
rapidly  
significa

TA



within the normal limits through the continued transpiration of the functional top; however, values declined following attack and subsequent disturbance of crown physiology. In polled trees, oleoresin exudation pressures declined due to the depletion of soluble solids following the removal of the top, which prevented transpiration and increased respiration (Table IX).

Changes in the levels of CO<sub>2</sub> and O<sub>2</sub> in gas sample units attached to trees reflected the internal respiratory performance of the bark. When units were attached above and below a girdle, the proportion of CO<sub>2</sub> below the girdle declined 10 days after treatment, parallel to the decline in the respiratory rate of the bark at this time. These changes are depicted in Fig. 12.

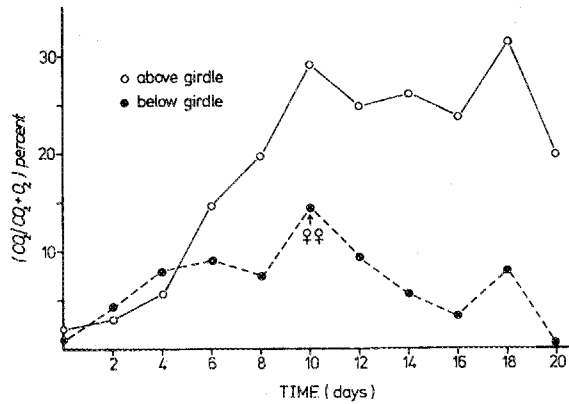


Fig. 12.—The ratio of CO<sub>2</sub> to CO<sub>2</sub> + O<sub>2</sub> in the air external to bark tissue above (○) and below (●) a girdle made at 3 m in a 20-cm dbh *P. radiata* tree. The area below the girdle was attacked on day 10.

No differences were obtained with respect to the proportions of the various monoterpenes; however, greater amounts of these materials and greater volumes of water were obtained from around treated than untreated trees. In preliminary studies, the frequency of attack on trees baited with 2% solutions of a-pinene in acetone and hexane, contained in 500-ml glass jars fitted with screw caps and cotton wicks, was 0.10 and 0.31 compared to an expected frequency of attack of 0.05 and 0.03 on untreated trees in 1968-69 and 1969-70 respectively.

The rate of moisture loss through the bark of felled trees achieved a maximum rate that differed with the presence and absence of branches. The maximum rate was achieved some 6-10 days after treatment, and the rate of water loss declined rapidly (Fig. 13). The rate of water release from the tissue below a girdle increased significantly after 10 days in comparison to the release from above the girdle (Table X).

TABLE X. Change in weight of anhydrous CuSO<sub>4</sub> held in vials attached to the bark tissue above and below a girdle. Values expressed relative to control rates of mg.m<sup>-2</sup>.h<sup>-1</sup>

	Time after treatment (days)				
	0	2	4	9	15
Above	107.5	16.1	40.0	35.0	2.7
Below	145.0	35.0	118.0	113.0	312.0

Losses in moisture from billets were proportional to the initial moisture content; billets of high moisture content had higher rates of water loss than drier billets. Rate of loss was also proportional to the intensity of drilling made by *Sirex* through the bark surface.

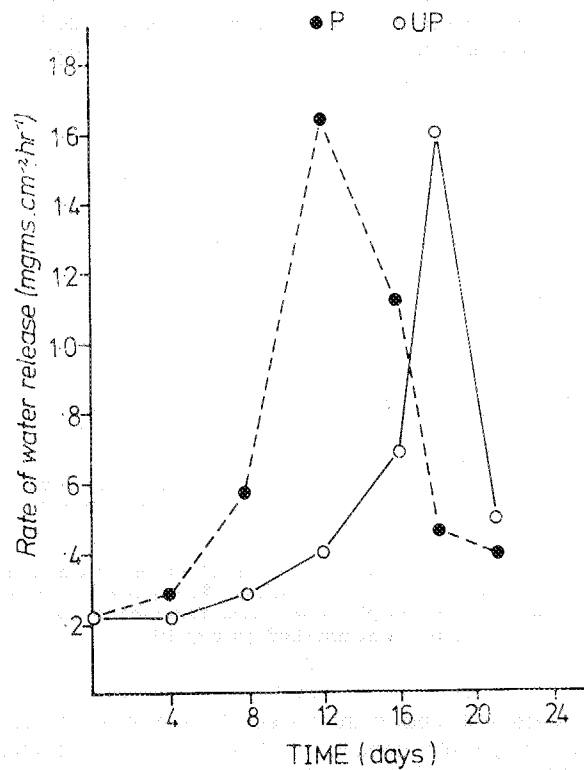


Fig. 13.—Rate of water release (change in weight of anhydrous  $\text{CuSO}_4$ ) from pruned (P) and unpruned (UP) 2-m long *P. radiata* billets held at 20°C in the laboratory.

### Discussion

Various types of damage to *P. radiata*, either singly or in combination, cause immediate changes in the trees' physiological processes. Stomata open and water is lost through the needles with a consequent increase in the water tension of the entire system. These changes result in an impairment of translocation but not photosynthesis as starch accumulates in the needles. Coutts (1969a & 1969b) demonstrated that the mucus secreted by the *Sirex* female during oviposition inhibited translocation, and it must therefore act to reinforce the initial stress condition. Needle respiration is increased by as much as 30% and, in the absence of labile photosynthate, the condition of stress is transferred to the bark, causing increased respiratory rates. The duration and degree of the changes depends upon the intensity of the initial stressor or damage and the physiological condition of the tree at that particular time. Thus, damaged trees were more likely to be attacked than undamaged trees and subdominant and suppressed trees were more prone to attack than dominant and codominant trees.

In this study that a critical permeability effect was observed in the days of the study in a dense forest in Washington in the pattern of attack.

The supply of water activity as a result of increased (Madden) it was shown that respiratory loss with respect to diurnal fluctuations was maximal. The study by Madden (1969) size. The pattern of normal physiological characteristic on stressed trees pers. comm. and solvent extraction information).

The short-term response above a given level of an apparent turgor relationship increment.

Therefore, under normal conditions are too low to be reached when in bark tissue releasing moisture and the amount which in turn the probability of trees the probability of tree's reaction.

Madden (1969) yet characterized between the trees other than in combination together with while the yield is low and loss increases of water loss trees. Similar permeability of resulted in attraction (Madden).

Therefore, from the study (L. 2395)

In this study it was demonstrated in the conditioning and girdling experiments that a critical stage may be achieved, usually some 10 days after treatment, when the permeability of the bark is critically affected. The physiological constancy of this effect was demonstrated by both respiratory and dendrometric change at different times of the year. The cessation of diameter activity in the expanded condition at 10 days in a defoliated *P. radiata* tree is shown in a dendrographic pattern recorded in Washington State in 1924 (MacDougal, 1925), and a similar phenomenon appears in the patterns of decapitated balsam poplar stems (Greenidge, 1962).

The suppression of diameter activity is related to an inhibition of cambial activity as the torque required to shear isolated discs of phloem progressively increased (Madden, in press). Following this stage and the climacteric in respiration, it was shown that the permeability to water of the bark tissue and the release of respiratory by-products was increased. The dendrograph patterns and respiration rates with respect to height indicate that there is a region in the stems of trees where diurnal fluctuations in diameter are minimal and phloem respiration rates are maximal. The height of this region is dependent on the diameter or size of the tree. Madden (1974) reported that the height of maximum attack was related to tree size. The present findings suggest that it is in this region that any disturbance to normal physiology is first experienced with subsequent alteration of permeability characteristics, release of volatiles and woodwasp attack. Air drawn from gas traps on stressed trees contain quantities of the monoterpene hydrocarbons (R. Simpson, pers. comm.), and positive responses by *Sirex* to trees baited with monoterpenes and solvent extracts of bark tissue have been obtained (Madden, 1968, and unpublished information).

The short term (48-72-h) reduction in the osmotic pressure of bark sap from above a girdle at 8-11 days is considered, after Bennett-Clark (1959), to represent an apparent decline due to the influx of water into cells. Normal osmotic and turgor relationships are restored following the initiation of cell expansion and diameter increment.

Therefore, it is postulated that the host-tree contains attractive materials, which under normal physiological conditions are only released from the tree at rates that are too low to stimulate the *Sirex*. Under conditions of stress, a situation may be reached where the rate of release of these volatile materials is increased via increases in bark tissue permeability. Thus, trees that are under any kind of stress are releasing more water vapour, respiratory gases and volatiles to the environment, and the amount of these materials is related to the degree and duration of stress, which in turn is related to the physiological status of the individual tree. Therefore, the probability that a given tree will be attacked is increased, and in a population of trees the probability of attack is going to vary in both space and time according to each tree's reaction to the stress.

Madden (1971) described a number of surgical treatments that resulted in different yet characteristic patterns of attractiveness to the woodwasp. Although no correlation other than in a general way, the patterns of water loss from the various treatments, together with the volatiles, does provide a possible explanation. Thus, in felled trees, while the yield of steam volatiles is high, the rate of water loss through the bark is low and as oil yield declines through oxidation to resin acids, the rate of water loss increases to a maximum and then declines through water depletion. The pattern of water loss coincides approximately with the pattern of attractiveness of felled trees. Similarly, in girdled trees, attractiveness does not commence until the permeability of the bark below the girdle to water is increased. Scorching the stems of trees resulted in the immediate loss of water, as steam, and volatiles and immediate attraction (Madden, 1968).

Therefore, it appears that patterns of attractiveness of *P. radiata* to *Sirex* result from the simultaneous release of water vapour and attractive volatiles through the

(L 2395)

F

bark and that the rate of release of these materials is dictated by the permeability of the bark.

The suitability of a tree as an oviposition substrate involves assessment by the woodwasp. Madden (1968, 1974) found that the female wasp regulated egg-laying according to the osmotic status or diffusion pressure deficit of the bark. Dominant trees with very high osmotic pressures ( $> 16 \times 10^5$  pascals) were rarely attacked and if attack did occur, the tree was soon rejected. However, at lower values, the inoculation of the tree primarily with mucus (Coutts, 1969b) will tend to further debilitate the tree. As the osmotic pressure falls due to the inhibition of translocation and the exhaustion of respiratory substrates, more eggs are laid.

Hillis & Shaine (pers. comm.) have shown by the use of labelled  $\text{CO}_2$  that it is the labile photosynthate and not reserve carbohydrate that is incorporated into the polyphenol-resin resistance reaction. Thus impaired translocation reduces the tree's ability to resist *Sirex* attack. It has been shown by dye infusion and forced *Sirex* attack that penetration into xylem elements experiencing high water tensions results in a marked invasion, in the latter case, of these elements with air. The water content of tissue surrounding oviposition drills increased with time after oviposition, and the presence of drills in the bark increased the loss of water and volatiles from the bark. The extent of drying from the drill containing mucus and arthrospores is more extensive than the drill containing an egg, and this difference arises from the nature of the surface of the respective drills. The surface of the drill containing mucus and arthrospores consists of broken tracheids, etc., whereas the drill that contains an egg is coated with a secretion that prevents the withdrawal of water from the vicinity of that drill (unpublished information). Therefore, drilling into stressed trees results in gross shifts in free water and hence in the hydration of tissues. The resin pressure falls and the greater degree of aeration favours the establishment and, collectively, the invasiveness of the fungus. In contrast, continued hydration in the vicinity of the lesion favours resin pressure and synthesis, resulting in the flooding of oviposition shafts with resin (Coutts & Dolezal, 1966a) and suppression of *A. areolatum* activity by monoterpene volatiles (Kile & Turnbull, 1974).

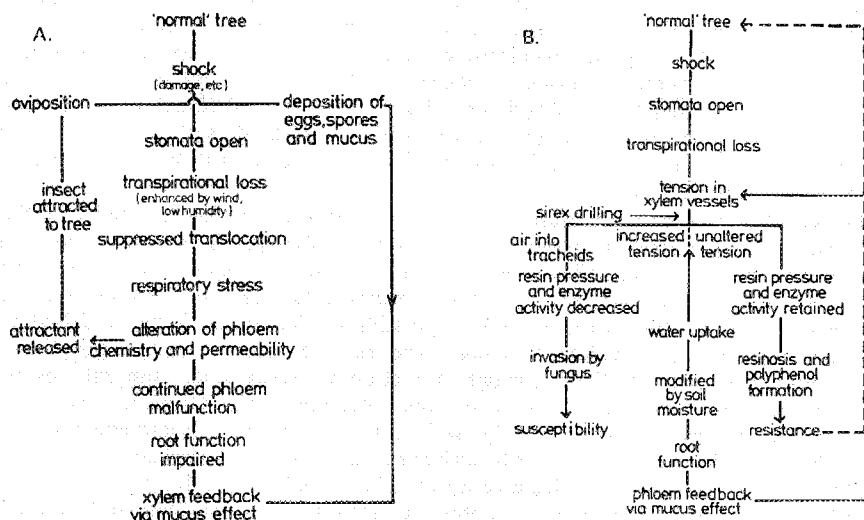


Fig. 14.—Possible sequence of changes occurring in the phloem (A) and xylem (B) that influence the attractiveness and susceptibility of individual *P. radiata* trees to *Sirex* attack.

This initi  
provided  
continues  
genetical  
individual

The se  
aerial port

Interpr  
mechanism  
their subse

#### Acknowledgements

The au  
helpful dis  
provided by  
The work

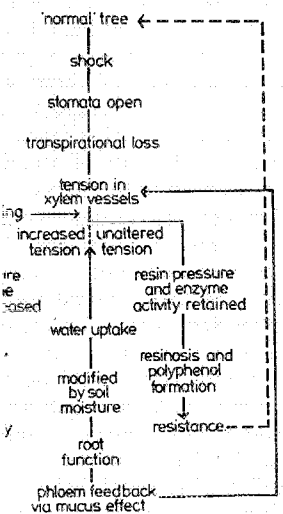
#### References

- BENNETT-CO  
PIL  
BORDEAUX,  
TH  
SYN  
COUTTS, M.  
no  
COUTTS, M.  
I.  
BIO  
COUTTS, M.  
II.  
COUTTS, M.  
Pin  
Le  
COUTTS, M.  
Pin  
FONG, L. K.  
was  
26,  
FRITTS, H.  
tree  
GILBERT, J.  
J. E.  
GRAY, H. R.  
GREENIDGE,  
vati  
JACKSON, D.  
N. Z.  
KILE, G. A.  
COD  
FOR  
KILE, G. A.  
twig  
FOR  
MACDOUGAL,  
tree  
MADDEN, J.  
Sirex

dictated by the permeability

involves assessment by the wasp regulated egg-laying of the bark. Dominant (scals) were rarely attacked however, at lower values, the (1969b) will tend to further the inhibition of translocation

use of labelled CO<sub>2</sub> that it is that is incorporated into translocation reduces the tree's infusion and forced *Sirex* high water tensions results with air. The water of water and volatiles from mucus and arthrospores is difference arises from the face of the drill containing etc., whereas the drill that is the withdrawal of water (n). Therefore, drilling into hence in the hydration of ee of aeration favours the ngus. In contrast, continued sure and synthesis, resulting tts & Dolezal, 1966a) and files (Kile *et al.*, 1974).



phloem (A) and xylem (B) individual *P. radiata* trees to

This initial resistance is reinforced further by the formation of fungistatic polyphenols provided the mucus effect is weakened and some translocation of photosynthate continues (Coutts & Dolezal, 1966a, 1966b). Resistance to the mucus effect is genetically determined but modified by season and the vigour characteristics of individual trees (Kile *et al.*, 1974).

The sequence of physiological events considered to be directly involved in the aerial portions of the tree and the bark and xylem tissues is summarised in Fig. 14.

Interpretation of the results of the investigation in the context of the postulated mechanism provides a workable explanation of the initial attractiveness of trees and their subsequent response to attack by *S. noctilio*.

#### Acknowledgements

The author thanks Mr. K. L. Taylor, Division of Entomology, C.S.I.R.O., for helpful discussion and for reading the manuscript. Invaluable technical assistance was provided by Mrs. G. Sanders, Miss B. Arman and Messrs. M. Storey and R. Bashford. The work was carried out with financial support from the National *Sirex* Fund.

#### References

- BENNETT-CLARK, T. A. (1959). Water relations of cells. pp. 105-191 in Steward, F. C. (Ed.) *Plant Physiology*. Vol. 2.—1st edn, 758 pp. New York, Academic Press.
- BORDEAUX, P. F. & SCHOPMEYER, C. S. (1957). Oleoresin pressure in slash pine. pp. 313-319 in Thimann, K. V. (Ed.). *The physiology of forest trees*.—678 pp. Harvard forest symposium, New York, Ronald Press.
- COUTTS, M. P. (1968). Rapid physiological change in *Pinus radiata* following attack by *Sirex noctilio* and its associated fungus, *Amylostereum* sp.—*Aust. J. Sci.* **30**, 275-276.
- COUTTS, M. P. (1969a). The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. I. Effects of the symbiotic fungus, *Amylostereum* sp. (Thelaphoraceae).—*Aust. J. Biol. Sci.* **22**, 915-924.
- COUTTS, M. P. (1969b). The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. II. Effects of *S. noctilio* mucus.—*Aust. J. Biol. Sci.* **22**, 1153-1161.
- COUTTS, M. P. & DOLEZAL, J. E. (1966a). Polyphenols and resin in the resistance mechanism of *Pinus radiata* attacked by the wood wasp, *Sirex noctilio*, and its associated fungus.—*Leaf. Commonw. For. Timb. Bur., Canberra* No. 101, 19 pp.
- COUTTS, M. P. & DOLEZAL, J. E. (1966b). Some effects of bark cincturing on the physiology of *Pinus radiata*, and on *Sirex* attack.—*Aust. For. Res.* **2**, 17-28.
- FONG, L. K. & CROWDEN, R. K. (1973). Physiological effects of mucus from the wood wasp, *Sirex noctilio* F., on the foliage of *Pinus radiata* D. Don.—*Aust. J. Biol. Sci.* **26**, 365-378.
- FRITTS, H. C. & FRITTS, E. C. (1955). A new dendrograph for recording radial changes of a tree.—*Forest Sci.* **1**, 271.
- GILBERT, J. M. & MILLER, L. W. (1952). An outbreak of *Sirex noctilio* in Tasmania.—*Aust. J. For.* **16**, 63-69.
- GRAY, H. R. (1944). Volume measurement of single trees.—*Aust. For.* **8**, 44-62.
- GREENIDGE, K. N. H. (1962). Dendrograph patterns in decapitated trees: preliminary observations.—*Can. J. Bot.* **40**, 1063-1071.
- JACKSON, D. S. (1955). The *Pinus radiata/Sirex noctilio* relationship at Rotoehu Forest.—*N.Z. J. For.* **7**, 26-41.
- KILE, G. A. & TURNBULL, C. R. A. (1974). The effects of *Radiata* Pine resin and resin components on the growth of the *Sirex* symbiont, *Amylostereum areolatum*.—*Aust. For. Res.* **6**, 27-34.
- KILE, G. A., BOWLING, P. J., DOLEZAL, J. E. & BIRD, T. (1974). The reaction of *Pinus radiata* twigs to the mucus of *Sirex noctilio* in relation to resistance to *Sirex* attack.—*Aust. For. Res.* **6**, 25-34.
- MACDOUGAL, D. T. (1925). Reversible variations in volume, pressure and movement of sap of trees.—90 pp. Pubn. 365. Washington, D.C. *Pubns. Carnegie Instn.*
- MADDEN, J. L. (1968). Physiological aspects of host tree favourability for the woodwasp, *Sirex noctilio* F.—*Proc. ecol. Soc. Aust.* **3**, 147-149.

- MADDEN, J. L. (1971). Some treatments which render Monterey pine (*Pinus radiata*) attractive to the wood wasp *Sirex noctilio* F.—*Bull. ent. Res.* **60**, 467–472.
- MADDEN, J. L. (1974). Oviposition behaviour of the woodwasp, *Sirex noctilio* F.—*Aust. J. Zool.* **22**, 341–351.
- MADDEN, J. L. (in press). Direct evaluation of cambial activity in trees.—*Aust. For. Res.*
- MOGREN, E. W. (1955). Silvical factors influencing resistance of Ponderosa Pine to Black Hills Beetle attack.—*Proc. Am. For. Ass.* **50**, 61–63.
- RAWLINGS, G. B. (1948). Recent observations on the *Sirex noctilio* population in *Pinus radiata* forests in N.Z.—*N.Z. J. For.* **5**, 411–421.
- SACHER, J. A. (1959). Studies on auxin-membrane permeability relations in fruit and leaf tissues.—*Pl. Physiol., Lancaster* **34**, 365–372.
- SCHOLLANDER, P. F., HAMMELL, H. T., BRADSTREET, E. D. & HEMMINGSEN, E. A. (1965). Sap pressure in vascular plants.—*Science, N.Y.* **148**, 339–346.
- SPRADBERRY, J. P. (1973). A comparative study of the phytotoxic effects of siricid wood-wasps on conifers.—*Ann. appl. Biol.* **75**, 309–320.
- UMBREIT, W. W., BURRIS, R. H. & STAUFFER, J. F. (1957). Manometric techniques and tissue metabolism.—2nd edn, 338 pp. Minneapolis, Minn., Burgess.
- WOLFE, J. C. & MAPLE, A. (1965). A technique for measurement of oleoresin exudation pressure in *Pinus radiata*.—*Aust. For. Res.* **1**, 41–44.

(Received 23 August 1976)

© Commonwealth Agricultural Bureaux, 1977

Bull.   
 With   
 Public

Descr   
 (Orth

R. F.   
 Centre

Intro

Zo

west a

biology

Toye,

Vuillat

to be

habits

paper,

of labor

Two

nymphs

the dry

dry sea

of the

wet sea

Method

Labora

Inse

near H