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Effect of fertilization and watering of Scots pine seedlings on the feeding preference of the pine weevil (*Hylobius abietis* L.)

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TIIVISTELMÄ: MÄNNYNTAIMEN LANNOITUKSEN JA KASTELUN VAIKUTUS TUKKIMIEHENTÄIN (HYLOBIUS ABIETIS) VIOITUKSEEN

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Two-year-old containerized Scots pine seedlings, raised under different fertilization and watering regimes, were subjected to feeding preference tests with the pine weevils in a bioassay. In the tests carried out with pairs of seedlings, the weevils preferred water-stressed seedlings to well-watered ones. In the case of well-watered seedlings, the weevils caused significantly more damage to NPK-fertilized seedlings than those given pure PK fertilization, or no fertilization at all. It is apparent that PK fertilization reduces, and water-stress increases, seedling susceptibility to weevil damage. The results support findings from field trials that water-stress (planting shock) predisposes seedlings to weevil damage. Weevil resistance is discussed with respect to fertilization and water stress as determinants of seedling quality.

Kaksivuotisia männyn paakkutaimia kasvatettiin taimitarhalla voimakkaasti lannoittaen (NPK tai PK) tai lannoittamatta sekä niukasti että runsaasti kastellen tukkimiehentäillä tehtäviä testejä varten. Ruukuissa kasvavia taimia vertailtiin pareittain laboratoriokokeissa. Tukkimiehentäi nakersi eniten niukasti kasteltuja, lannoittamattomia taimia. Runsaasti kastelluista taimista PK-lannoitettuja taimia nakerrettiin merkittävästi vähemmän kuin NPK-lannoitettuja tai kokonaan lannoittamattomia. Siten on mahdollista, että taimen PK-lannoitus vähentää ja vedenpuute altistaa tainta tukkimiehentäille. Saatu tulos tukee myös kentällä todettua seikkaa, että taimen istutusshokki (vedenpuute) voi altistaa tainta tukkimiehentäin vioitukselle. Taimen tuhonkestävyyttä tarkasteltiin välillisesti myös taimen metsänviljelykepoisuuden arviointiin käytettävien taimitunnusten avulla.

Keywords: pine weevil, *Hylobius abietis*, feeding preferences, *Pinus sylvestris*, fertilization, water stress.
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1 Introduction

The pine weevil (*Hylobius abietis* L.) feeds on the stem bark of Scots pine seedlings, and is one of the major causes of seedling mortality in young reforestation areas, if insecticides are not used (Eidmann 1974). Seedlings raised under different nursery conditions may differ in their susceptibility to weevil attack after planting. This topic has been discussed (e.g. Eidmann 1969, 1974, Selander and Immonen 1991, Selander (forthcoming)), but not much investigated.

The effects of nursery cultivation practices, and fertilization in particular, on the general outplanting success of pine seedlings have been widely studied (for literature, see Duryea 1984, Driessche 1984a, 1984b, Parviainen 1988, Troeng and Ackzell 1988, Lassheikki et al. 1991). It is evident that the final success of Scots pine seedlings is a result of many joint factors associated with the characteristics of individual seedlings (e.g. size, Rikala 1989) and their nutrient status (e.g. Christersson 1973, Rikala and Huurinainen 1990), the effects of handling (e.g. dehydration, water stress, Hallman et al. 1978, Kauppi 1984), terpene composition (Kalo et al. 1974, Selander and Kalo 1979) and the planting environment (e.g. influence of pests and diseases). Although the above studies do not confirm that any particular factors would affect seedling susceptibility to insect damage, they do provide useful information about the seedlings; how their physiological condition, nutrient and terpene concentrations and growth characteristics vary and develop after planting, and consequently change the food quality for the pine weevil.

Insect herbivory, particularly in respect to water and mineral stress of host, has been a major concern in many ecological studies (for literature, see White 1984, Gershenzon 1984, Brodbeck and Strong 1987, Mattson and Haack 1987, Mattson et al. 1988, Larsson 1989). Insect responses to fertilized or water-stressed plants constitute a complex situation which has mainly been studied on leaf-feeding insect species in their larval stage, and resulted in rather varying and conflicting results and hypotheses, that are hardly applicable to the pine weevil. In the case of *Hylobius* weevils, the insect/host herbivory relations are difficult to specify, because the adult insect does not depend on pine seedlings for reproduction or its (only) source of food, but can freely move and feed on the phloem and cambium tissues of fresh logging residues and other conifers (Eidmann 1974).

In our earlier studies we found differences with respect to weevil damage between naturally regenerated and planted seedlings (Selander et al. 1990), and between differently fertilized seedlings (Selander and Immonen 1991). Although the above studies offered a quite satisfactory approach for comparing general resistance in the field, we decided to determine the extent to which seedling fertilization or irrigation could vary weevil feeding preference in a bioassay. Studies aimed at attaining a better understanding of possible defense reactions in pine seedlings need comprehensive chemical studies, but it would be meaningful to carry out general comparisons between differently grown plants before investigating resistance mechanisms in detail.

2 Material and methods

2.1 Seedlings

Two-year-old Scots pine (*Pinus sylvestris* L.) seedlings were raised in a standard way in solid-wall plastic Enso trays (1Me-1Ae) in the Suonenjoki nursery (62°39'N, 27°03'E), Central Finland. Each tray consisted of 40 containers (180 cm^3). The seed originated from a natural stand (Karttula Stock T10-78-43). The seedlings were raised according to normal Finnish nursery practices using *Sphagnum* peat as the substrate and normal fertilization and irrigation during the first two growing seasons. No fertilizer was applied to the seedlings in the spring before they were removed from the trays and shipped in plastic bags to the Jokiniemi nursery in Vantaa (60°17'N, 25°03'E), Southern Finland, where the experiments were carried out from 7th June

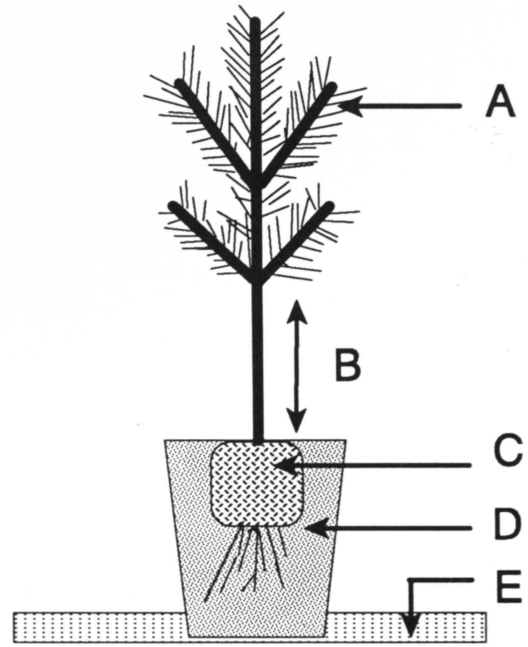

Fig. 1. The experimental setup used in raising and the test seedlings:
A. Needle samples (Table 3),
B. The stem section used in studying feeding preference in the bioassay,
C. Seedling root container (peat, Table 1),
D. Substrate (sand, Table 1),
E. Constant supply of water (seedling group A) and nutrients (seedling groups C and D, 7-Superex and 9-Superex, respectively, Table 1).

to 10th September, 1984.

About 500 seedlings were randomly divided into four groups and replanted in individual plastic pots (volume 1600 cm^3) (Fig. 1). Washed sand (Rudus Co., particle size 0.5–1.2 mm) was used as the substrate. Average concentrations of the main nutrients were analyzed in the sand and in the root ball (peat) of the seedlings (Table 1). The seedling pots were placed in small, open-wall greenhouses to protect them from rainfall, but to expose them to outdoor temperatures during the experiment.

The fertilizers and water were applied to the seedlings, starting from 7th June, in the following treatments, which correspond to the seedlings groups A,B,C and D, and later referred to as unfertilized, water-stressed, PK-fertilized and NPK-fertilized seedlings, respectively:

Group A: Unfertilized seedlings. The seedlings pots were sunk to a depth of 2–5 cm of water. No fertilizer was added to the water and no other means of watering was used. The purpose was to provide the seedlings with a constant water supply without the application of fertilizers (Fig. 1). The only nutrients available were those originally present in the sand and root ball (Table 1).

Group B: Water-stressed seedlings. Instead of placing the pots in a constant water supply as above, the water supply was kept to a minimum. Only 100 ml of pure water per plant was applied to the surface of sand in the pots at two-week intervals. No other source of water was available. This watering regime was designed to provide the seedlings with the smallest possible water supply without causing any wilting symptoms.

Group C: PK-fertilized seedlings. The seedling pots were treated as in group A. Instead of pure water however, a 0.05 % aqueous solution of Kekkilä 7-Superex (N 0 %, P 16.0 %, K 20.0 % and micronutrients) served as the fertilization medium (Table 1).

Table 1. Concentrations of nutrients available for the test seedlings in the root container, sand substrate and the liquid medium.

Substrate	N	P	K	Ca	Mg	Fe (mg/l)	Bo	Cu	Mn	Zn	Mo
Peat	42	6.4	50	1000	300	300	0.1	6.7	6.1	-	-
Sand	30	3.0	15	500	35	35	0.1	6.7	2.6	-	-
7-Superex 0.05%	0	80	100	0	12	12	0.14	0.07	0.5	0.12	0.01
9-Superex 0.05%	133	27	100	0	1.0	1.0	0.14	0.07	0.5	0.12	0.01

Table 2. Morphological characteristics of the differently fertilized seedlings at testing time.

Seedling group	n	Stem diameter, mm		Height, cm		100-needle dry weight, g
		Mean	S.D.	Mean	S.D.	
A. No fertilization	96	3.1[a]	0.4	7.8[a]	1.8	0.5
B. No fertilization, water-stress	96	3.2[a]	0.6	9.6	3.3	0.5
C. PK fertilizer	96	3.1[a]	0.5	7.4[a]	2.0	0.6
D. NPK fertilizer	96	3.5	0.5	7.3[a]	1.8	2.1

[a] No significant difference between means in Tukey's test $P < 0.05$ (Norusis 1989)

Table 3. Average nutrient concentrations of the needles of differently fertilized seedlings at testing time.

Seedling group	N	P	K	Ca	Mg
			mg/g		
A. No fertilization	8.6	1.23	6.87	2.35	1.44
B. No fertilization, water stress	12.6	1.74	6.48	2.20	1.39
C. PK fertilizer	10.6	2.70	10.89	2.85	1.86
D. NPK fertilizer	20.9	4.60	21.37	4.65	2.64

Group D: NPK-fertilized seedlings. The seedlings in the pots were treated similarly to groups A and C, but the liquid fertilization medium consisted of 0.05 % Kekkilä 9-Superex (N 19.4 %, P 5.3 % K 20.0 % and micronutrients) (Table 1).

The nutrient solutions were replaced weekly with fresh ones. The pH values of the water in groups A and B ranged from 6.2 to 7.0, in group C 5.4–6.6, and in group D 5.3–7.0.

Before removing the seedings for tests, their morphological characteristics were assessed: height, stem diameter and 100-needle dry weight (Table 2). The nutrient status of the seedling groups was evaluated by determining the average nutrient concentration in the needles (Viljavuuspalvelu Oy, Soil Analysis Service Ltd., Table 3).

2.2 Collection and storage of test insects

About 2000 pine weevil specimens were collected from a sawmill in Suonenjoki during their swarming period in May. The test weevils were stored at 5 C° in glass jars (volume 400 ml), 50 insects in each container. There was a layer of moist sawdust on the bottom of jars. Fresh pieces of bark were provided for food during the storage period. Males and females were separated on the testing day and exposed to room temperature (20–22 C°) for about one hour before the beginning of the test.

2.3 Test procedure

The feeding preference of the weevils was tested by exposing the stems of two differently grown seedlings to the weevils in acrylic "sandwich" cages, measuring 24.0 × 8.0 cm in outer diameters and an inner volume of 340–380 cm^3, depending on the size of the stem sections (Fig. 2). Three weevils were placed in each cage where they could freely feed on either of the seedlings. The test lasted for 20 hours, lasting from noon until the following morning. Males and females were tested in separate cages. Each weevil and seedling pair were used only once. The test took place in the open-wall greenhouses where the seedlings were grown.

At the end of the period, feeding damage on the bark surface was recorded by outlining the feeding traces on paper wrapped around the

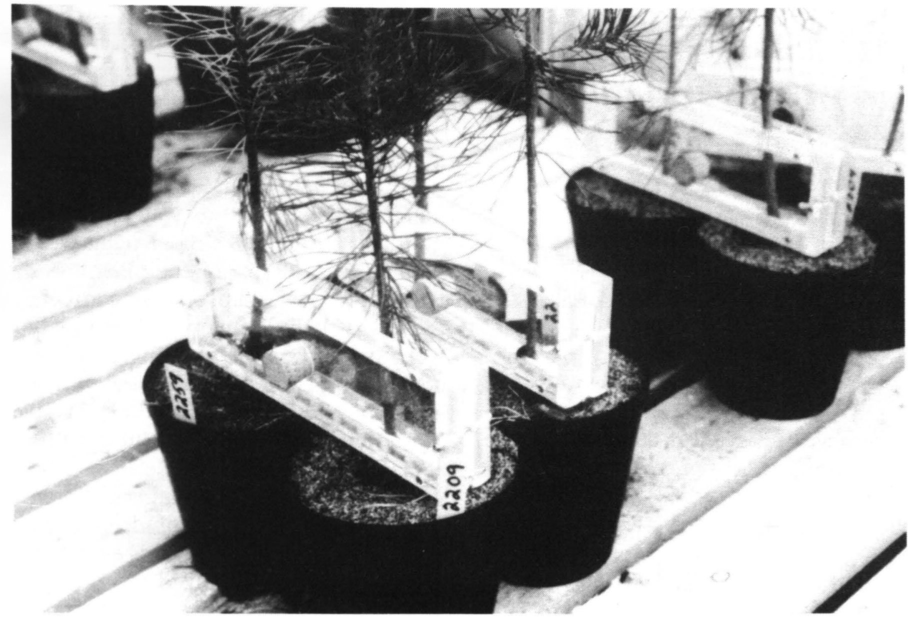

Fig. 2. View of the cages used for comparing feeding preference in the bioassay.

stem. The feeding area was later measured using transparent graph paper.

Two distinct types of feeding, which also resulted in two types of bark damage, were observed during the bioassay. The superficial type of feeding was characterized by discontinuous "tasting-type" feeding on the outer bark surface which resulted in only spot-like or superficial wounding on the bark surface. The other type of feeding, here called "deep feeding", was characterized by more continuous feeding at the same spot, resulting in larger and more openly damaged bark lesions where the entire phloem tissue was deeply exposed. Both types of damage were assessed separately.

The seedlings groups were tested by pairs in all combinations (A-B, A-C, A-D, B-C, B-D and C-D). There were 32 seedling pairs in each combination. A total of 384 seedlings, 96 seedlings per group, were tested using 1152 weevils. The tests were performed during a three-week period (13.7–4.9.1984). Equal numbers of seedlings from all groups were taken for testing each time.

3 Results

3.1 Quantity of damage on the seedlings

The test procedure proved to be successful: when the weevils were let into the test cage, they could move around freely, could taste both plants and begin feeding on either plant. The average damaged bark area varied by seedling groups from 3.5 % to 10.5 % of the bark surface exposed in the cage for 3 weevils during 20 hours. Male and female weevils did not differ in their feeding, and their results were combined.

The weevils fed most actively on the unfertilized, stressed seedlings (Group B): 80.2 % of them were affected, averaging 0.65 cm^2 bark surface per seedling. In the other seedling groups, damage occurred on 69.6 % of the well-watered, unfertilized seedlings (A) (0.42 cm^2), 63.5 % of the PK-fertilized (C) (0.21 cm^2), and 66.7 % of the NPK-fertilized seedlings (D) (0.50 cm^2). According to the average total amount of bark damage, the PK-fertilized seedlings (D) were significantly less damaged than the other

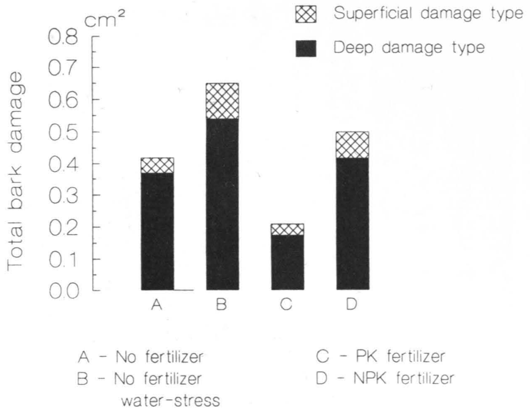

Fig. 3. The average damaged bark area in differently grown seedlings.

groups (Fig. 3). On the other hand, the damaged area on the NPK-fertilized seedlings (D) did not differ significantly from the unfertilized seedlings (A or B).

The deep damage type was predominant on all the seedlings, but both damage types were distributed in almost the same proportions in the seedling groups: the deep damage type accounted for 85.1–88.2 % of all the bark damage by seedling groups, the rest being of the tasting type (Fig. 3).

Each seedling group was exposed to the weevils three times: once with each of the three counterpart groups. In these repetitions, the area of damaged bark seemed to be rather similar irrespective of which other seedling group served as the counterparts. However, more damage occurred on the stressed plants (B) when tested with the unfertilized ones (A) or the PK-fertilized ones (C) than with the NPK-fertilized plants (D) (Fig. 4).

3.2 Feeding preference between seedling pairs

In the tests designed to determine which plant in the pair was preferred, using the Wilcoxon matched-pair test (Norusis 1989), unattacked seedlings were included as zero-damaged. Arranging the data in this way resulted 192 seedling pairs: in 6.3 % neither plant was attacked, in 47.4 % of the pairs one plant was damaged, and in 46.4 % both plants were affected.

Relatively little superficial (tasting type) damage occurred on the seedlings, and only in one test combination was there a significant difference: the NPK-fertilized seedlings (D) were more superficially damaged than the unfertilized ones (A) ($P < 0.05$) (Fig. 4).

The weevils showed rather different feeding preference in the case of deep damage type: stressed seedlings (B) were significantly preferred to their unfertilized (A) or PK-fertilized (C) counterparts. The weevils also preferred unfertilized seedlings (A) to PK-fertilized ones (C), and NPK-fertilized (D) to PK-fertilized (C) seedlings. On the other hand, no significant difference was found between unfertilized (A and B) and NPK-fertilized ones (D).

The box plots (Fig. 4) showed that there were considerable differences in the size of the damaged area on individual seedlings raised under the same conditions: all seedling groups contained some seedlings where the damaged area was considerably larger than that on the other seedlings (Fig. 4, * and o marks). This deviation was taking fully into account by using Wilcoxon tests. However, it remained uncertain whether this was due to variation in seedling attractiveness, or occurred because some weevils were exceptionally voracious on some occasions.

4 Discussion

In this bioassay study, water-stressed seedlings suffered greater damage than the well-watered ones. This supports our field results (Selander et al. 1990) where newly planted seedlings, which usually suffer from water stress (cf. Hallman et al. 1978, Kauppi 1984, Parviainen 1988), were more frequently attacked than their naturally grown, well-established counterparts.

Water stress in seedlings is usually associated with poor root-soil contact and low overall root activity (cf. Kramer 1983, Hale and Orcutt 1987). Seedling root activity has been suggested to serve as an useful indicator of potential seedling field performance (for literature, see Lassheikki et al. 1991, Mattsson 1991). Our results suggest that root activity indicators (e.g. root growth

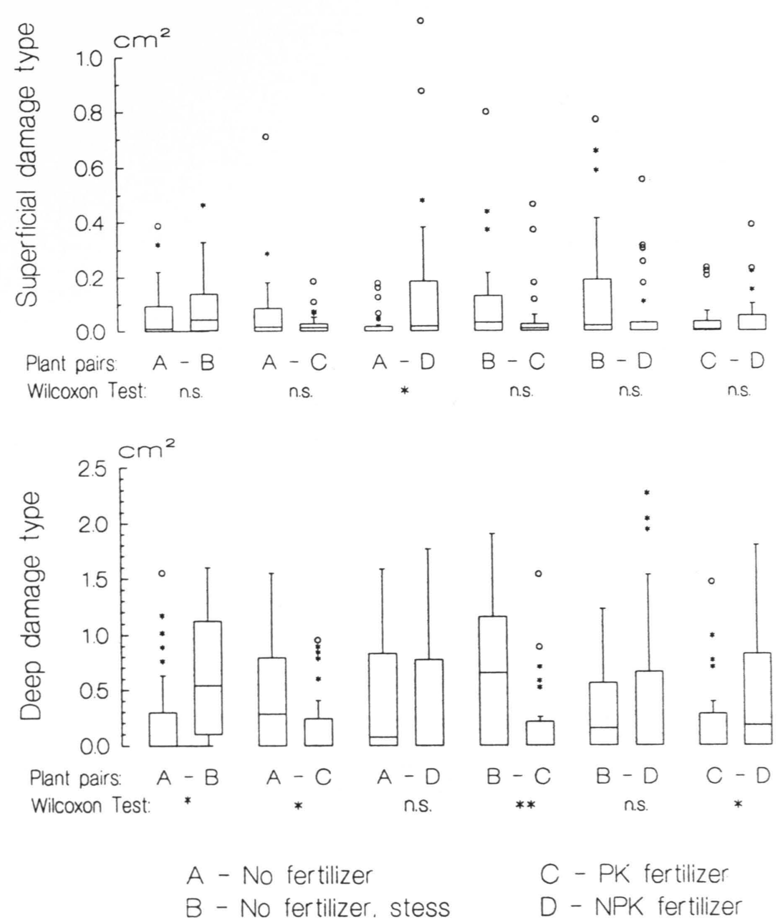

Fig. 4. Feeding preference of the pine weevil between different seedling pairs. Box plot diagrammes (Wilkinson 1990) show the bark area affected by two damage types in seedlings tested in pairs: The values of damage area which ranges from 25 % to 75 % percentiles in the data is illustrated as graphic boxes, the median value as the cross line in the box, and the solid line extending outside the box show is the range of values which fall outside 1.5 times of the box length. The outlier values which do not fall under the previous categories are plotted individually: marked with an asterisk (*) when larger than 1.5 × interquartile range, or with an empty circle (o) when larger than 3 times the interquartile range. Statistical tests were carried out by using the Wilcoxon matched-pair signed-ranks test (Norusis 1989): ** = $P \leq 0.01$, * = $P \leq 0.05$, n.s. = $P > 0.05$.

capacity measurements) may be be planned for evaluating weevil resistance together with seedling field performance, because water stress can predispose seedlings to weevil damage. Our findings are contradictory to the results of Lekander and Söderström (1969), who considered water-stressed seedlings to be more weevil resistant than those with a normal water balance.

Water stress apparently changes pine oleoresin composition and lowers oleoresin exudation pressure (for literature, see Gershenzon 1984, Mattson and Haack 1987). Hodges and Lorio (1975) and Gilmore (1977) reported that water stress affected monoterpene concentrations in loblolly pines by increasing α-pinene and decreasing limonene, myrcene and ß-pinene. According to Nordlander (1987, 1990, 1991), limonene in particular inhibits attraction to α-pinene, which is the principal attractant for the pine weevil (Selander et al. 1973), especially in synergism with ethanol (Tilles et al. 1986). It would be interesting to study whether water stress causes changes in the limonene, α-pinene, or possibly ethanol concentrations in Scots pine seedlings, and to try to determine the olfactory properties of stressed seedlings in particular. Another point of further interest is to determine whether the possible decline in oleoresin exudation pressure in stressed seedlings affects weevil feeding preference.

Growing the seedlings under a PK fertilization regime, without any nitrogen, reduced weevil feeding preference in the present study. This is in accordance with our findings in the field, where the PK-fertilized seedlings were less damaged than the NPK-fertilized ones (Selander and Immonen 1991). Comparison between the same seedling groups (although similarly named) should be done with care, because the seedlings were raised using different methods and the seedlings thus had different growth characteristics. For example, the needle nitrogen concentration in the bioassay seedlings was extremely high (20.9 mg/g, Table 3) compared those in the field study (9.6–12.8 mg/g, Selander and Immonen 1991, Table 2).

The NPK-fertilized seedlings were rather different in some characteristics: their stems were thicker, their needle N, P, K and Ca concentrations were considerably higher than those in the other groups (Table 2), and their needle dry weight was about four times larger (Table 3). These characteristics agree with the widely reported effects of nitrogen fertilization: an increase in pine needle size (e.g. Kellomäki et al. 1982) and carbohydrate reserves, which are apparently essential in early root development (Puttonen 1986) and drought resistance (Ritchie 1984). According to Hiltunen et al. (1975), nitrogen fertilization increased the relative quantity of total terpenoids in pines and causes some changes in the concentrations of individual terpenes, but did not alter the attractiveness of trap bolts to the pine weevil (Löyttyniemi and Hiltunen 1976). On the other hand, nitrogen fertilization has also been found to affect terpene composition in grand fir seedlings, but fertilization did not change the overall yield of terpenes (Muzika et al. 1989).

There were some differences in the superficial and deep feeding types between differently grown seedlings. The superficial form was more pronounced in the NPK-fertilized seedlings compared with the unfertilized ones. NPK-fertilized seedlings have thicker phloem (cf. Selander and Immonen 1991), which may provide the weevils with plentiful food without their needing to feed on the innermost parts of the phloem. Although the two forms of feeding cannot be completely distinguished, they are still useful in elucidating weevil feeding in relation to possible plant responses. Gref and Ericsson (1975) reported that wounded seedling bark had increased resin-acid concentrations. Ericsson et al. (1988) showed that weevils avoid feeding on wounded stem sections, and prefer to feed, when there are earlier wounds on the stem bark, on the section of bark lying above the old scars. In our study, the superficial feeding, rather than the deep feeding, may be a sign of a defensive reaction by seedling bark. Closer study of the different forms of weevil feeding may help in understanding the weevil-plant interactions.

These results showed that seedling fertilization and water status have a considerable effect on the feeding preference of the pine weevil. It is therefore important that seedling vitality, particularly in connection with fertilization and water relations, is carefully clarified in weevil resistance studies.

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