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Breeding for Weevil Resistance in Norway Spruce

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Introduction

Plantations of white pine (Pinus strobus L.) and Norway spruce (Picea abies [L] KARST.) located in the eastern part of Canada and U.S.A. are seriously attacked by the white pine weevil (Pissodes strobi PECK). The extensive damage caused by this native insect is of considerable economic importance, as natural regeneration of white pine exposed to full daylight is also subject to heavy attack. Many of the present white pine stands are composed largely of forked and crooked trees of little value, and in plantations damage seems even more severe. "The loss in stumpage value during the last half century amounts to millions of dollars. In the Adirondack region in New York, the weevil has injured Norway spruce plantations so severely that they are practically worthless," CRAIGHEAD (1950). The white pine weevil is at the moment under intensive study by Canadian entomologists.

If this insect were introduced to the Norway spruce stands of Europe it might well become as serious a pest as it is in the extensive white pine forests of the Northeast. It is to make the European foresters familiar with this potential enemy of the Norway spruce stands in Europe that this paper has been prepared. The paper deals with the damage pattern in Norway spruce, a general discussion of weevil resistance, and how weevil resistance might be obtained by means of species hybridization.

1. Damage pattern in Norway spruce

The Norway spruce plantations visited while travelling in Ontario, Quebec, New Brunswick, the New England States and the Lake States leave a very varied impression regarding weevil damage. It is only in a few areas that the weevil is absent and the Norway spruce undamaged. Commonly the weevil is present and damage considerable. Where Norway spruce has been underplanted or is in heavy competition with shrubs, weevil damage is usually slight. It is in the "successful" well kept plantations that weevil damage is most severe. Indeed, up to the age of 25 years most of these plantations are a sorry sight, and one may wonder whether any useful timber will be produced. The fact remains, however, that many older stands display a reasonable appearance. This might result from slender co-dominants eventually monopolizing the site, when early stout dominants become weevilled and weakened, or from the fact that Norway spruce can shoot from side buds on the leader, and generally has a strong tendency to develop only one leader in place of the one lost. In the latter respect, it differs strikingly from the damage pattern in white pine. The white pine has no side buds on the middle part of the leader, and the side branches compete for a longer period before one of them expresses dominance. However, before the Norway spruce reaches timber size the value of the log might be decreased considerably by crooks and bends.

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a. Observation of weevil damage in a plantation of Norway spruce at the Petnwawa Forest Experiment *Station*

A study (HOLST, 1954) was made in a plantation of Norway spruce planted in 1924 with 2-2 stock, probably of southern German origin. The plantation was thinned heavily after a severe winter frost damage in 1934-35, and only 24 well spaced trees were left of the 1500 originally planted. Because of the open stand the trees have green branches from the ground, making branch type and crown type easily recognizable and comparable. It was therefore fairly easy to estimate the genotypic crown types, as described by SYRACH LARSEN (1947). Under such favourable conditions even a relatively small number of trees gives a fairly accurate picture of the form factors involved.

Each of the 24 trees were classified as to diameter at breast-height, height, height-diameter ratio, crown diameter, branching habit and weevil damage.

b. Results

It was found that trees with broad crowns were more often weevilled than those with narrow crowns and trees with low height-diameter ratio were more often weevilled than those with high height-diameter ratio.

A relation was also found between height-diameter ratio and height above ground of the first damaged leader. Stout trees were all damaged earlier than slender trees.

The comb spruce had larger crown diameters and showed heavier weevil damage than the brush types. The plain spruce type was not found in this material.

For the material investigated it appeared that slender genotypes with narrow brush-type crowns are associated with light weevil damage, while stout genotypes with broad comb-type crowns tend to be severely damaged by the weevil.

c. Discussion

The underlying causes for slender genotypes being more resistant than broad genotypes must remain obscure until the results of more detailed investigations are available from the entomologists. However, slender leaders seem to be of importance in this respect. PREBBLE (1951) studying white pine weevil damage on white pines at the Petawawa Forest Experiment Station found that susceptibility increases with leader length and leader diameter, and that for the trees in the most susceptible classes, attack in any one year frequently exceeded 70 percent and occasionally exceeded 90 percent. HEIMBURGER (1953) working with selection of weevil resistant white pines found smaller leader diameters on grafts produced from scions of apparently resistant trees than on the grafted controls.

It also appears from an as yet incomplete study of weevil damage in a local Norway spruce provenance experiment, that slender crowns are associated with slender leaders, and it is reasonable to assume that the slender genotypes of Norway spruce reported above also had slender leaders. However, slender leaders may perhaps be induced on non-slender genotypes. In the material investigated, three of the trees were double stemmed and

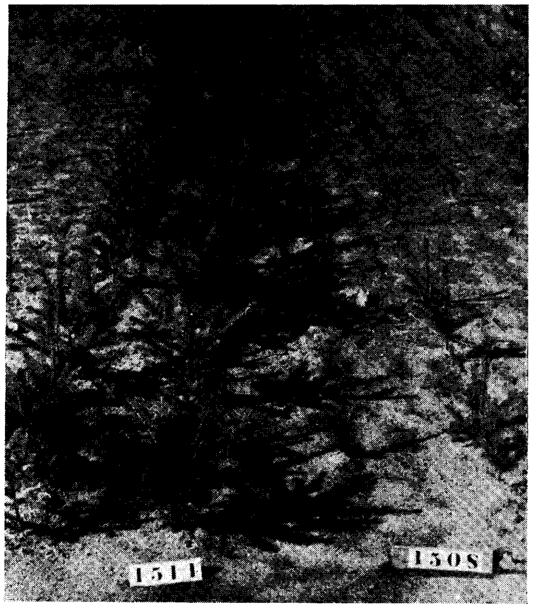

Fig. 1. Comparison of 2-2 Norway spruce seedling. — S. 1511—51 is a one parent progeny from a broad-crowned and heavily weeviled tree. S. 1508-51 is a one parent progeny from a slender and almost resistant tree.

because of this, extremely slender. They were highly resistant to weevilling. Of the six stems involved, three were weevilled within the last year, while the other three showed no sign of injury.

It should be remembered, however, that what has been reported above is a relative resistance and not immunity. Although PLUMMER and PILLSBURY (1929) experimentally proved that weevils prefer large and dominant leaders, they also made the statement "that to a certain extent infestation may be based on chance", his statement being based on observations that trees appearing susceptible are not attacked and vice-versa. It is therefore quite possible that severe weevil damage might occur in plantations made up of only slender leader genotypes or of offspring of apparently resistant genotypes. However, this last point has to be proven, and is at the moment being studied by means of controlled hybridization and vegetative propagation of slender resistant genotypes of Norway spruce. Open pollinated single tree progenies of the 24 Norway spruces investigated above show some striking differences. 2-2 seedlings originated from the slender and resistant genotypes are smaller and of less bushy appearance than those of the broad and susceptible genotypes.

2. What is weevil resistance?

The problem arises as to whether some internal factors have an influence on the weevil susceptibility of Norway spruce. With a species so heavily attacked by an insect that feeds on such a large variety of species in both pine and spruce, this possibility seems unlikely at first consideration. However, some of the results obtained are difficult to explain if some internal factors are not involved. The following is a brief discussion of how internal weevil resistance could occur.

Weevil resistance may be due to an antagonism between insect and host species. It is usually explained as a special composition of an element in the tree which is repellent to the insect when it attempts to feed, lay eggs, or hatch eggs, in certain species. The resistance of white spruce (*Picea glauca* [MOENCH] Voss.) is considered as belonging to this group. On the advice of ANDERSON (1953), a smell preference test was made with ground white spruce and Norway spruce needles. It was quite apparent that the weevils, avoided the white spruce smell. A similar test made of resistant and susceptible Norway spruces did not indicate a smell preference for susceptible individuals.

A relative weevil resistance occurs where the weevil will feed on and lay eggs in certain species, but where the eggs or larvae, or both, are pitched out or walled off before any serious damage to the leader can occur. This kind of resistance has been reported by MILLER (1950) who studied the damage pattern of the pine reproduction weevil *(Cylindrocopturus eatoni* BUCH.*)* on the Jeffrey-Coulter pine hybrid *(Pinus Jeffreyi* × *Coulteri)*. A similar resistance has been observed by SULLIVAN (1953) in Scots pine plantations in the Petawawa area.

Another type of resistance is found only during a particular period of the life cycle. For instance, very little weevil damage is found during the first years after the establishment of white pine and Norway spruce plantations, and it is believed that the leaders are of a form or size disagreeable to the weevil. The study of MILLER (1950) indicates that weevil attack is not a stable character in some species. He found that a group of Jeffrey pine which resisted strong attacks in 1947, were killed in 1948. This and other similar cases indicated "that changes in the physiological condition of a tree may result in susceptibility". The resistance of the Jeffrey-Coulter pine hybrid showed no fluctuation due to seasonal changes and this seems to be an inherited character introduced from the Coulter pine.

Finally there is the question whether weevil resistance is correlated with place of origin and whether a suitable choice of seed source would give a higher resistance. BALDWIN (1949), reporting on a series of Norway spruce provenance experiments planted near Hillsboro (New Hampshire), could find no distinctive growth form nor any form of special resistance to the white pine weevil. The same general statement could be made of the provenance experiment located near Ely, Wisconsin, which was visited by the author in 1952. However, overtopping weed trees in both cases were probably responsible for generally low attacks (below 10%). A summary of the weevil damage tallied in a local Norway spruce provenance experiment is shown in Table 1. The damage ranges from 14% to 80% and there is apparently no damage cline in existence. However, a few provenances of good growth have remarkably low damage. If these provenances continue to show consistantly low damage, it might be worthwhile to try them out on a larger scale and in other environments.

It has been reported by A. H. MACANDREWS, Professor of Forest Entomology, New York State College of Forestry, that the leader of a certain Norway spruce at Wanakena, N. Y., survived weevil attacks year after year while all surrounding trees suffered repeated attacks. Grafts and cuttings from this tree were made, but became subject to weevil injury when they reached four feet in height. He concluded that the factor of immunity was not genetical as it was not passed on from ortet to ramets, and that the original immunity may have been closely associated with the environment. As weevil resistance seems closely related with the physiological balance, a change of this balance, which is known to occur in grafts and cuttings, could account for this. But what would have happened if a number of immune trees were crossed and the offspring

Table 1
Incidence of weevil attack on Norway spruce of various origins and growth rates

Incidence below average			Incidence above average		
Seed lot	Origin	% Damaged	Seed lot	Origin	% Damaged
Height growth 0.41 to 0.50 feet per year					
S. 206—40	Valea Mare, Roumania	16	S. 86—39	Burtnieki District, Latvia	30
S. 199—40	Småland, Sweden	20	S. 84—39	Proulx, Quebec	36
Height growth 0.31 to 0.40 feet per year					
S. 16—37	Öst Agder, 200-400 m, Norway	15	S. 193—40	Pokljuka, Yugoslavia	34
S. 196—40	Poland	16	S. 17—37	Öst Agder, 0—200 m, Norway	36
S. 203—40	Pförten, Germany	17	S. 200—40	Schwarzwald, Germany	46
S. 207—40	Ivanovsk District, U. S. S. R.	21	S. 35—38	Telemark, 100—300 m, Norway	80
S. 195—40	France	23			
S. 13—35	Riga, Latvia	23			
S. 194—40	Valen Bistrei, Roumania	26			
S. 205—40	Tacau-Fata Strajei, Roumania	27			
Height growth less than 0.31 feet per year					
S. 204—40	Inntröndelag, Norway	4	S. 198—40	Freinisberg, Switzerland	39

placed in an environment similar to that in which the parents grew?

The problem of whether resistance in Norway spruce is genetically determined or due to the influence of the environment is difficult to decide. Both factors seem to be operative, sometimes one being more important than the other. The above study indicates that a genetical form factor is associated with weevil resistance, but the material also indicates that internal, and not clearly understood, factors play an important role, and these again either can be inherited, or controlled by the environment.

It is likely therefore that some increase in resistance might be accomplished by means of selection and controlled breeding. Immunity, however, is not likely to be produced by intraspecific hybridization.

3. Breeding for weevil resistance by means of species hybridization

Species hybridization seems to offer greater possibilities for the creation of weevil resistant Norway spruce hybrids. We shall confine the discussion here to those species of spruce on which weevil attack has been observed. Other exotic spruces may have resistance, but they have either not been tried on a sufficiently large scale to obtain definite information about them, or we are ignorant of such trials. There is a considerable variation in weevil resistance in the spruces native to the North American continent. MacAloney (1932) lists the following spruces according to severity of attack:

Severely — Norway spruce — *Picea abies* (L.) Karst.
Commonly — red spruce — *Picea rubens* Sarg.
Occasionally — black spruce — *Picea Mariana* (Mill.) B. S. P.
Rarely — Colorado spruce — *Picea pungens* Engelm.
white spruce — *Picea glauca* (Moench) Voss.

In the Rocky Mountain region and in the Pacific Northwest considerable damage is done to Sitka spruce *(Picea sitchensis* [Bong] Carr.) and Engelmann spruce *(Picea Engelmanni* [Parry] Engelm.) by respectively the Sitka spruce weevil *(Pissodes sitchensis* Hopk.) and the Engelmann spruce weevil *(Pissodes engelmanni* Hopk.). Both weevils work in the terminals and have a life history similar to that of the white pine weevil. Damage on Sitka spruce is so severe in Oregon and Washington that planting of this species has largely been discontinued. Whether Sitka spruce and Engelmann spruce are resistant to the white pine weevil is an open question. Sitka spruce grows very poorly in the east and Engelmann spruce, being a high elevation type with very high precipitation requirements, does not do well either. However, realising the close relationship of the eastern and western weevils, resistance to the white pine weevil in Sitka spruce and Engelmann spruce is not to be expected.

The reason that Colorado spruce is rarely attacked by the white pine weevil is obscure, but MacAloney's observation of the high resistance of this species in the New England States can also be confirmed for trees planted in Ontario and Quebec.

White spruce is highly resistant to weevil damage. The nature of this resistance is not clearly understood, but it has locally been demonstrated in smell tests that the weevil constantly migrated to the source of Norway spruce odour. The author has tentatively tried to explain the high resistance of white spruce by a particular resin complex found in white spruce that has an antagonistic effect on the weevil both with respect to ovoposition and survival of larvae. It is suspected that this resin compound is related to the characteristic "cat smell" of the white spruces. However, the mechanism of the weevil resistance of white spruce needs further investigation. An interesting point is that the white spruce of the east has a much stronger "cat smell" than the white spruce found in the Prairie Provinces. The significance of this at the moment is not clear, as western white spruce provenances planted in Ontario and New Brunswick have not been attacked by the local white pine weevil populations. On the other hand, forest insect surveys in Canada have consistantly reported more weevil damage on white spruce in the Prairie Provinces. It might well be that there are special strains of (white pine) weevil outside the white pine distribution area which are able to survive on a white spruce diet, and the white spruces of the Prairie Provinces might be of moderate resistance. A future check in the still young provenance experiments in the east and planting of eastern white spruce in the Prairie Provinces might in time give results of interest for solving this problem.

The difference in susceptibility of red and black spruce is difficult to account for. These two spruces hybridize quite frequently in the east and must therefore have a considerable gene exchange. When found pure in natural stands they show marked ecological differences. Red spruce is adapted to grow in competition with hardwoods. In its natural habitat it grows in dense shade, a habitat very unfavourable to weevils. Selection pressure for weevil resistance has therefore been slight. When planted in open plantations it is very susceptible to weevil damage. Black spruce on the other hand is less tolerant and is usually found in pure stands in swamps. It has therefore been subjected to weevil attack and is more resistant than red spruce.

This survey of the damage pattern of the native spruces indicates that there is a great variation between species and that the source of resistance for production of weevil resistant Norway spruce types should be sought in white spruce or Colorado spruce. As Colorado spruce is an exotic in the east and has been planted only on a very limited scale the choice must be in favour of the white spruce. The problem is then: can the weevil resistance of the white spruce be transferred to Norway spruce?

The first attempt to transfer the weevil resistance from white spruce to Norway spruce was to make a set of species hybrids of these two species. In three successive seasons Norway spruce was crossed with eastern, middle and western Canadian white spruce. Reciprocal crosses were made with middle and eastern Canadian white spruce using a variety of Norway spruce pollen mixtures. No viable seed were obtained from these extensive crosses. This incompatibility is in accordance with the results reported by WRIGHT (1953). The hybrids previously reported by JOHNSON and HEIMBURGER (1946) do not in their seventh growing season show any sign of hybridity. This is unfortunate because, had it been possible to break the incompatibility barriers only once, chances would have been good for recombination by means of back crossing to both parent species. The evidence of the experiments to date is that Norway spruce and white spruce hybridize with difficulty or not at all.

It is therefore necessary to try a new approach. One promising possibility is to use Sitka spruce to establish a crossing bridge for transfer of genes for weevil resistance from white spruce to Norway spruce. The Sitka × white spruce hybrid is quite common in Denmark (LARSEN, 1945; TAARUP, 1945; and BORNEBUSH, 1946) and is also found in a limited area where the two species meet on the Kenai Peninsula in southern Alaska (LITTLE, 1953). SYRACH LARSEN (1937) produced this hybrid by controlled pollination in 1933. In the same year he selfed a natural hybrid and backcrossed it to white spruce. The hybrid has also been produced in Sweden (EKLUNDT EHRENBERG, 1943; KIELLANDER, 1953) and in Germany (LANGNER, 1952). This hybrid is fertile and can be produced without difficulty, probably most readily with Sitka spruce as female.

The Sitka × white spruce hybrids and their back crosses to Sitka spruce have been on trial at the Petawawa Forest Experiment Station, but they were not hardy. The seed was of Danish origin and the white spruce component has definitely been of eastern Maritime origin, probably from New Brunswick. As the New Brunswick white spruce is not quite hardy at Petawawa, it would probably be too much to expect frost hardiness of Sitka × white spruce hybrids where both components have originated in a Maritime climate, one western, the other eastern. Neither have the hybrids produced in Schmalenbeck been hardy here. It has therefore been necessary to produce a more hardy hybrid by crossing boreal white spruce (provenance Cochrane, Ontario) with British Columbia Sitka spruce. The interest in the Sitka × white spruce hybrid is three fold. First, the "cat smell" reported above is transferred to the hybrid. Secondly, it is planned to test the hybrid for resistance to *Pissodes sitchensis* in British Columbia. Thirdly, LANGNER (1952), in Forstamt Flensburg, found natural Sitka × Norway spruce hybrids, and later produced this hybrid by controlled pollination and obtained heterotic offspring. Chances are therefore good for the establishment of a crossing bridge: white spruce — Sitka spruce — Norway spruce.

Material is then available in one form or another to establish the crossing bridge for transfer of weevil resistance from white spruce over Sitka spruce to Norway spruce. Theoretically it should be possible, and future plans are to make Norway × (Sitka × white) or (Norway × Sitka) × (Sitka × white) for study of the inheritance of weevil resistance and for the possible transfer of genes for resistance from white spruce to Norway spruce.

Another interesting possibility is to use *Picea Koyamai* SHIRAS. WRIGHT (1953) has shown that this primitive Japanese species hybridizes readily with almost any of the more complex species, and also with species that are mutually incompatible, such as Norway spruce and white spruce. *Picea Koyamai* is furthermore more hardy than Sitka spruce and for this reason should be easier to work with in the continental climate of Petawawa. It also appears that *Picea asperata* MAST., and probably also *Picea glehnii* (FR. SCHMIDT) MAST. belong to this group.

At present, these methods of obtaining weevil resistance in Norway spruce are being explored as a part of the tree breeding work at the Petawawa Forest Experiment Station. This special type of "resistance breeding" has been taken up, not only to solve the most important pest problem of one of our most important exotics, but also because it creates an opportunity to explore resistance breeding as such, and to clarify the problems involved in species hybridization with this most important spruce, the white spruce.

Summary

The paper has been prepared to make the European forester aware of a potential insect enemy of the European Norway spruce *(Picea abies)* stands. Plantations of white pine *(Pinus strobus)* and Norway spruce located in the eastern part of Canada and U. S. A. are seriously attacked by the white pine weevil *(Pissodes strobi)*. A survey is made of the damage pattern in Norway spruce and the value of somewhat resistant slender genotypes with narrow brush-type crowns is stressed. A discussion is made of types of weevil resistance in forest trees and of whether a resistance cline is found in Norway spruce. It is concluded that a small increase in resistance might be accomplished by means of selection and controlled breeding in Norway spruce, but that breeding for weevil resistance by means of species hybridization seems more encouraging. The reasons for weevil resistance, and variation in degree of resistance, of different native and exotic spruces are discussed. It is pointed out that the source for breeding weevil resistance into Norway spruce is to be found in white spruce *(Picea glauca)* and Colorado spruce *(Picea pungens)*. As Norway spruce do not cross readily with white spruce, it is suggested to establish a crossing bridge with the help of Sitka spruce *(Picea sitchensis)* or *Picea Kojamai*.

Zusammenfassung

Titel der Arbeit: *Züchtung auf Rüsselkäfer-Resistenz bei Fichte.* — Durch die Arbeit wird die europäische Forstwirtschaft auf ein Schadinsekt in den Beständen der europäischen Fichte aufmerksam gemacht. Pflanzungen von Stroben *(Pinus strobus)* und europäischen Fichten *(Picea abies)* in Ost-Canada und im Osten der USA werden ernstlich durch den Stroben-Rüßler *(Pissodes strobi)* gefährdet.

Ein Überblick über das Ausmaß des Schadens bei europäischen Fichten wird gegeben (vgl. Tabelle 1). Es wird auf die Bedeutung wenigstens einigermaßen resistenter Genotypen hingewiesen, die im übrigen schwächlich sind und schmale bürstenförmige Kronen besitzen. Allgemeines über die Rüsselkäfer-Resistenz bei Waldbäumen wird diskutiert, ferner Spezielles über Resistenzmöglichkeiten bei der Fichte. Es wird geschlossen, daß eine leichte Resistenzsteigerung durch Selektion und kontrollierte Züchtung bei der Fichte erreichbar ist, daß aber die Züchtung auf Rüsselkäfer-Resistenz mit Hilfe von Artbastardierung erfolgversprechender zu sein scheint. Die Gründe für die Käfer-Resistenz und ihr wechselndes Ausmaß bei verschiedenen einheimischen und exotischen Fichten werden besprochen, und es läßt sich vermuten, daß Voraussetzungen für eine Käfer-Resistenz-Züchtung für die europäische Fichte bei der Weißfichte *(Picea glauca)* und bei der Coloradofichte *(Picea pungens)* zu finden sind. Da aber die europäische Fichte nur schwer mit der Weißfichte kreuzbar ist, wird der Versuch zur Schaffung einer Kreuzungsbrücke mit Hilfe der Sitkafichte *(Picea sitchensis)* oder der *Picea Kojamai* vorgeschlagen.

Résumé

Titre de l'article: *L'amélioration de l'épicéa, en ce qui concerne la résistance à Pissodes strobi.* —

Cet article attire l'attention de la sylviculture européenne sur un coléoptère parasite des plantations d'épicéas européens en Amérique. Comme les plantations de *Pinus strobus,* celles de *Picea abies* dans l'Est du Canada et des U.S.A. sont menacées sérieusement par *Pissodes strobi.*

Un aperçu de la grandeur du dommage fait aux épicéas européens est donné par la table 1. On indique la proportion des génotypes ayant une résistance plus ou moins grande; mais ils sont peu vigoureux, avec des cimes étroites et des ramules en brosse. La résistance des arbres forestiers, en général, aux pissodes et spécialement celle des épicéas est discutée. On en conclut qu'une faible augmentation de résistance peut être obtenue par une sélection et une amélioration contrôlée des épicéas, mais qu'une hybridation interspécifique promet plus de succès. Les causes de la résistance aux attaques des coléoptères et la variabilité de la résistance des épicéas autochtones et exotiques sont discutées et on peut supposer qu'on trouvera, avec *Picea glauca* et *Picea pungens,* une base pour l'amélioration des épicéas européens. Mais, comme l'hybridation de l'épicéa européen avec *Picea glauca* est difficile, on propose d'atteindre ce but en passant par une hybridation intermédiaire avec *Picea sitchensis* ou *Picea Kojamai.*

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