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Factors affecting transfer and spread of *Phellinus weirii* mycelium in roots of second-growth Douglas-fir

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Effects of site, root diameter, soil depth of interroot contact, length of root surface in contact, type of contact, and relative position of roots were investigated on the frequency of transfer of *Phellinus weirii* (Murr.) Gilbertson mycelium between roots and its spread along roots of second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Successful transfer of *P. weirii* as ectotrophic or endotrophic mycelium occurred in 32 and 3%, respectively, of total number of interroot contacts. Unsuccessful transfers occurred in 4 and 62%, respectively, with the balance of contacts having undetermined transfers, owing to extension of mycelium to the root collar of both roots in contact. A *Pseudotsuga–Polystichum* site had a higher frequency of unsuccessful transfer than two *Pseudotsuga–Gaultheria* sites. Average root diameter was greater and average depth was less in contacts with successful transfers than in those with unsuccessful transfers. Type or length of contact or relative position of roots had no significant effects on transfers. There was a highly significant inverse relationship between root diameter and length of endotrophic mycelial spread as measured by decay column. The regression of endotrophic on ectotrophic mycelial spread along roots was highly significant for both proximal and distal spread. In most roots, ectotrophic mycelium had spread distally to the tip and proximally to the stump, whereas endotrophic mycelium had not.

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On a étudié les effets de la station, du diamètre des racines, de la profondeur à laquelle elles se touchent dans le sol, de la longueur de leur surface de contact, du type de contact et de leur position relative, sur la fréquence de transmission du mycélium de *Phellinus weirii* (Murr.) Gilbertson entre les racines et sur la propagation de ce champignon le long des racines des jeunes pousses de Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco). La transmission de *P. weirii* par son mycélium ectotrophique ou entrophique s'est produite respectivement dans 32 et 3% du nombre total de contacts entre les

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racines. Elle ne s'est pas produite respectivement dans 4 et 62% de ce nombre. Elle était indéterminée dans les autres cas, du fait de l'extension du mycélium au collet des unes et des autres racines en contact. Dans une station de *Pseudotsuga–Polystichum* il y a eu une plus haute fréquence d'insuccès de la transmission de *P. weirii* que dans deux stations de *Pseudotsuga–Gaultheria*. Le diamètre moyen des racines était plus grand et la profondeur moyenne moindre dans les contacts où la transmission se produisait que dans ceux où celle-ci n'avait pas lieu. Le type ou la longueur de surface de contact, de même que la position relative des racines, n'ont pas eu d'effets significatifs sur la transmission du champignon. Il y a eu une corrélation inverse très significative entre le diamètre des racines et la distance de propagation du mycélium endotrophique, telle que mesurée en fonction de la colonne de pourriture. La régression de la propagation du mycélium endotrophique sur celle du mycélium ectotrophique le long des racines a été très significative tant pour la propagation proximale que pour la propagation distale. Dans la plupart des racines le mycélium ectotrophique s'était propagé d'une manière distale vers les extrémités des racines et d'une manière proximale vers la souche, tandis que le mycélium endotrophique ne s'était point propagé.

[Traduit par le journal]

Introduction

Phellinus weirii (Murr.) Gilbertson, the most destructive disease of second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in the Pacific northwest, spreads primarily by ectotrophic mycelium growing along root surfaces of susceptible species. It has been established that the fungus is transferred from one root to another by root contact (Wallis and Reynolds 1965), but the frequency of successful transfer across contacts or the effects of site or type, size and depth of contact, or root diameter have not been reported. Using wood of several tree species, Wallis and Reynolds (1962) proved that ectotrophic mycelium could penetrate uninjured bark. Distal or proximal spread of the fungus endotrophically in wood from the point of inoculation varied considerably and was related to the direction of the most extensive ectotrophic mycelium, but the relationship has not been quantified. K. M. Reynolds and W. J. Bloomberg (unpublished data[2]) found the probability of root contact was dependent on site factors, including soil depth, stoniness, and slope, and on stand factors, including tree dbh and stand density.

A full understanding of the basic dynamics of the disease must be based on the identification and assessment of factors determining transfer of the fungus across root contacts and its subsequent spread along roots. The objectives of the present study were to investigate the frequency of transfer of *Phellinus* root rot between roots and the effects of the following factors on transfer and spread: site, root diameter, depth in soil, position of roots relative to one another, type of contact, and the amount of root surface in contact. The relationship of endotrophic to ectotrophic mycelial spread along roots was also investigated.

Methods

Nineteen plots were selected in three areas near Cowichan Lake, B.C. (Table 1). Area 1 was a gently sloping (average 20%) *Pseudotsuga–Polystichum* site (McMinn 1960) with moderately stony soil averaging 1 m deep. Area 2 was a fairly level *Pseudotsuga–Gaultheria* site with very stony soil up to 50 cm deep underlain by hardpan. Area 3 was a steeply sloping (average 50%) *Pseudotsuga–Gaultheria* site with many soil boulders and an average soil depth of 50 cm.

Plots, 10 m in diameter, were located on the margins of infection centres caused by *P. weirii* (Wallis 1976). In each plot, two to six sample trees, 1–4 m apart, showing moderate to severe crown symptoms of *P. weirii* infection, were selected for examination. The average age (31–40 years) and the average dbh (23.0–24.8 cm) were similar for all areas. Root systems of sample trees were hydraulically excavated to expose infected roots for the full length of infection. Methods and equipment used for excavation were the same as those used by K. M. Reynolds and W. J. Bloomberg (unpublished data[2]). The following information was recorded for each contact between a diseased root and other contacting roots: diameters of both roots at contact point, depth in soil, length of root surface in contact, relative root contact position, i.e., roots one above the other or in the same horizontal plane, and length of live ectotrophic or endotrophic *P. weirii* mycelium extending proximally or distally along each root from point of contact. Ectotrophic and endotrophic spread were determined from visible surface mycelium and extent of wood decay, respectively. Mycelium was identified as *P. weirii*, using the criteria of Wallis (1976). Contact type was classified as follows: graft, roots deformed, e.g., surface flattened by contact, contact without deformation, and near contact, i.e. less than 5 mm between roots. A contact was classified as intratree if both roots belonged to the same tree and as intertree contacts if they were from different trees. Transfer of ectotrophic mycelium (spread from one root to another) was classed as unsuccessful if mycelium occurred on only the diseased root at the contact point. It was classed as successful if mycelium occurred on both roots but did not extend to the root collars of both roots, and as undetermined if mycelium extended to the collars of both roots. This classification recognizes the possibility that two roots in contact may have been infected through their respective parent boles rather than from the contact; otherwise, it assumes that the only other source of infection was by root contact. None of the roots examined made contact with primary *P. weirii* inoculum, e.g., stumps or roots from the previous stand. Transfer of endotrophic mycelium within the wood of roots, as evidenced by decay, was recorded in the same manner as for ectotrophic mycelium.

[2]Reynolds, K. M., and W. J. Bloomberg. Factors affecting inter-tree root contact in second-growth Douglas-fir.

TABLE 1. Root diameter and size and depth of root contacts and transfer of *Phellinus weirii* in second-growth Douglas-fir in three sites

			Root contacts				Transfers (%)					
							Ectotrophic mycelium			Endotrophic mycelium		
Site[a]	No. plots	No. trees	No. examined	Avg. root diam[b] (cm)	Avg. depth (cm)	Avg. length (cm)	Successful	Unsuccessful	Undetermined	Successful	Unsuccessful	Undetermined
1	6	15	47	4.0(1−23)	25.4**(5−60)	5.8(1−20)	43	14	43	9	63**	28**
2	2	7	34	2.6(1−10)	19.6(10−35)	3.3(1−15)	24	5	71	0	29	71
3	11	38	114	3.0(1−13)	20.1(7−50)	3.6(1−25)	30	0	70	2	25	73

[a]See text for description of sites.
[b]Measured at point of contact.
**Denotes significantly greater ($p \geq 0.1$) than values in other areas.

Data were analyzed by multivariate analysis (Dixon and Brown 1979) to determine significant differences among areas and between transfer success classes with respect to all factors examined. Differences among means were tested by the multiple range test or *t*-test. Relationships between ecto- and endo- trophic mycelial spread and between root diameter and mycelial spread were tested by linear regression.

Results

Of a total of 195 contacts examined, transfer as ectotrophic mycelium was successful in 32%, unsuccessful in 4%, and undetermined in 64% (Table 1). Comparable results for transfer as endotrophic mycelium were 3, 35, and 62%, respectively.

Type or length of contact or relative root position had no significant ($P = 0.05$) effect on transfer success. Areas did not differ significantly with respect to frequency of contact type. The majority of contact types were those without root deformation (51%); the next most frequent were those with root deformation (39%). Grafts and near contacts accounted for 4 and 6%, respectively.

Depth of root contact was significantly less (20.4 vs. 31.2 cm) and root diameter was significantly greater (8.7 vs. 2.4 cm) in contacts with successful transfer of ecto- or endo- trophic mycelium than in those with unsuccessful transfer. The percentage of intratree contacts with successful transfer as endotrophic mycelium was significantly higher (11.8 vs. 6.6%) than in intertree contacts. The depth of intertree contacts was significantly greater (22.7 vs. 18.5 cm) than those of intratree contacts.

The regression of endotrophic on ectotrophic mycelial spread was highly significant ($P = 0.01$) for both proximal and distal directions (regression coefficients 0.14−0.61, intercept values −0.97 to −19.41). Maximum distance between ectotrophic and endotrophic mycelial fronts was 160 cm. In most roots examined, ectotrophic mycelium had spread distally to the tip and proximally to the root collar (Table 2). About 5% or less had no mycelial spread. In the remainder, mycelium had spread to variable distances from the contact point. In areas 1 and 2, a higher percentage of roots had no endotrophic spread than full length spread proximally, and in area 2, distally also. There was a highly significant inverse linear relationship between endotrophic spread and root diameter.

Discussion

About one-quarter to one-half of the 195 root contacts examined resulted in successful transfer of ectotrophic mycelium from one root to another. In addition, the one-half to three-quarters of contacts in which transfer success was undetermined probably included a high percentage of successful transfers. It is probable there-

TABLE 2. Percentage of roots with full length or no spread of ectotrophic or endotrophic mycelium in *Phellinus weirii* infected Douglas-fir

		Ectotrophic				Endotrophic			
		Proximal		Distal		Proximal		Distal	
Area	No. roots	Full length	Nil	Full length	Nil	Full length	Nil	Full length	Nil
1	66	69.1	5.4	64.9	5.4	20.6	58.5	42.6	48.3
2	49	82.3	5.9	73.5	4.4	27.9	69.1	25.8	69.1
3	162	45.3	0	71.9	0	44.3	42.1	46.5	42.5

fore, that a large majority of root contacts resulted in successful transfer of ectotrophic mycelium from one root to another. The major factors in transfer failure appear to be too small a root and too great a depth in the soil. Wallis and Reynolds (1962) were unable to find any effect of root diameter in spread of ectotrophic mycelium from inoculations, but endotrophic spread in wood of uninjured roots was inversely related to root diameter. Nelson (1967) found that *P. weirii* in cubes of Douglas-fir stemwood survived longer at 25- and 50-cm depths than at 7.5- and 15-cm depths. He attributed the longer survival at greater depth to decreased antagonistic microflora. Wallis and Reynolds (1965) found that roots growing in the duff layer were seldom overgrown with *P. weirii* mycelium, whereas those at greater depth were extensively invaded.

Absence of the fungus therefore, would not explain the decrease in successful transfers with increasing soil depth. Distal portions of large roots and small roots which would tend to lie deeper in the soil may be killed or weakened by *P. weirii* infections at the root collar or in other parts of the root system. These roots would probably be invaded by secondary fungi, rendering them unsuitable substrates for transfer of *P. weirii*. Although the difference in average soil depth between successful and unsuccessful transfers was relatively large, the proportion of unsuccessful was small, so it can be assumed that such factors, as a whole, play a minor role in transfer of the fungus.

According to the regression estimates of endotrophic on ectotrophic mycelial spread, ectotrophic mycelial fronts would precede endotrophic fronts by an average of 1.2−31.8 cm. This relationship is consistent with Wallis and Reynolds (1965) finding that ectotrophic mycelium preceded decay by a few centimetres in small roots. The maximum distance between fronts of 160 cm is also consistent with their finding of a maximum distance of 200 cm in large roots.

Differences among sites included more unsuccessful mycelial transfers in area 1 than in the other areas and was probably related to the deeper soil and, consequently, greater depth of contacts in area 1. Greater endotrophic spread in area 3 was not explained by differences in root diameter relative to the other sites. Higher frequency of successful transfers in intratree than intertree contacts did not appear to be related to any other factors and suggests some undefined interaction between fungus and host.

It is concluded that frequency of successful transfer of *P. weirii* between roots as ectotrophic mycelium is very high and is relatively little affected by site or root factors. Successful transfer of the fungus as endotrophic mycelium is much less frequent.

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