ARMILLARIA MELLEA AND MORTALITY OF BEECH AFFECTED BY BEECH BARK DISEASE[1]

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Abstract.--The role of Armillaria mellea in the mortality of beech trees affected by beech bark disease was determined by excavating root systems of beech trees infested by beech scale, Cryptococcus fagisuga, or also infected by the bark fungus, Nectria coccinea var. faginata. Only trees infected by Nectria showed any effect on the root system. They had fewer 4th-order nonwoody branch roots and less starch than trees only infested by scale. A. mellea colonized roots only on Nectria-infected trees and was consistently found on roots associated circumferentially with areas of stem bark necrosis caused by Nectria. Complete colonization by A. mellea of the root system of dying trees occurred infrequently. The majority of trees were partially colonized and colonization occurred after stem necrosis. A. mellea did not accelerate mortality in those stands affected by beech bark disease.

INTRODUCTION

In studies on beech bark disease, aerial photos and ground examination showed that many diseased American beech, Fagus grandifolia Ehrh., persisted for several years, although a few trees died within 1 year (Houston 1974). Excavation of these trees at the root collar showed that Armillaria mellea (Vahl ex Fr.) Kummer (Armillariella mellea (Vahl. ex Fr.) Karst.) had girdled the root collar region of the trees that died within 1 year. It was absent from the root collars of the diseased trees that had symptoms but persisted (personal communication, D.R. Houston). This suggested that beech bark disease predisposed some trees to infection by A. mellea and that the fungus affected the rate of tree death in beech stands affected by beech bark disease.

Attack of trees by A. mellea has been consistently associated with stress factors that apparently predispose them to attack by this fungus (Wargo 1980a). Stress, such as defoliation, can cause changes in the root tissues of the chemical constituents that can stimulate growth of A. mellea (Wargo 1972) and increase susceptibility of roots to infection by this fungus (Wargo and Houston 1974).

Beech bark disease could be effecting similar changes in the root system. Trees stressed by the scale, Cryptococcus fagisuga Lindinger (C. fagi Bar.), and bark fungus, Nectria coccinea var. faginata Lohman, Watson and Ayers, could also be attacked by A. mellea, killing the tree faster than if it were affected by beech bark disease alone. If A. mellea affected the rate of mortality it would also affect the rate of subsequent deterioration of the trees, and the root fungus would have to be considered in formulating plans to manage stands affected by beech bark disease.

This study was done to determine the status of A. mellea in the roots of beech and assess its role in stands where beech bark disease was killing trees.

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MATERIALS AND METHODS

Stands of beech, infested with beech scale and currently infected by N. coccinea var. faginata, were located in the "killing front" (Shigo 1972) in northeastern and north-central New York on the eastern and western edges of the Adirondack Preserve, and in the "advancing front" in north-central Pennsylvania in the Tioga State Forest. Two stands in north-central New York were observed in July 1980 and two stands in northeastern New York and Pennsylvania were observed in June 1981.

Intensive root observations

In one stand in north-central New York, where high mortality was just occurring, 15 trees were selected for intensive observations on the root system. Five trees had zero to trace populations of beech scale (control trees) and five trees had heavy to very heavy scale, judged by the density of their white waxy excretion (Lonsdale 1980). None of these trees were infected by N. coccinea var. faginata. The remaining five trees were infected by N. coccinea var. faginata and had a range of scale infestations. Necrotic lesions in the bark with evidence of old or new perithecia and tarry spots verified infection.

On all 15 trees, three second-order woody branch roots (laterals) on each of four first-order woody lateral roots (buttress) were excavated until three first-order nonwoody roots having intact fibrous branches (<1 mm diam) were uncovered (terminology after Lyford 1975). This distance was usually 2 to 3 meters from the root-stem base. The living and dead 4th-order branches were counted on the three nonwoody roots from each lateral root. If the stele was cream colored or white when the bark was peeled it was counted as living, if it was brown it was counted as dead. Nonwoody branch roots on the next 60 cm of root on all the lateral roots were also counted.

The density of rhizomorphs of Armillaria mellea on the bark of the woody roots was estimated as absent, low, moderate or high. The bark tissue was then stripped to the wood on all excavated roots to locate necrotic lesions, mycelial patches of A. mellea, or decaying tissues.

A root sample was taken from each of three healthy woody roots from each of the 15 trees and their starch content was determined by the histochemical iodine technique (Wargo 1975). Starch content was used to judge the physiological condition (vigor) of each tree and relate it to scale and Nectria status.

Extensive root observations

In all six stands, beech trees that were dying or had recently died and were infected by N. coccinea var. faginata were selected for extensive observations on the root system. Trees were considered to have died recently if bits of leaves, twigs, and buds were present in the crown and the entire circumference of stem bark was necrotic but intact at the root-stem base. Dying trees had brown or green wilted and chlorotic foliage in the crown and only streaks of necrotic stem bark down to the root-stem base. In one stand in each area a site was chosen where at least five trees of each category could be observed on the same site. The status and pattern of A. mellea colonization observed on these trees was then verified by arbitrarily selecting trees in each category throughout that stand and a nearby stand. Evidence of Nectria infection, i.e. tarry spots, necrotic lesions, necrotic patches, and old or new perithecia; the extent of bark necrosis on the stem and its distence above the root-stem base; and the presence of decay were recorded. In addition, the chronology of crown death was reconstructed. The size of twigs and branches, remnants of leaves, tightness of the bark, and evidence of decay in the crown were used to judge whether the tree had died slowly in stages over several years or whether the whole crown had died rapidly during one year.

In one stand in New York, five trees that were infected by N. coccinea var. faginata and had dead portions of the crown but otherwise healthy foliage were also examined for colonization by A. mellea. Similar trees in each of the other stands were arbitrarily selected and examined to verify the initial observations.

On each tree, all the buttress roots were excavated to .50 to .75 meters from the tree. The density of rhizomorphs on their surfaces was estimated and the bark was peeled to locate areas colonized by A. mellea. If no colonization by A. mellea was observed, two roots on opposite sides of the tree were excavated to at least 2 meters. The bark was also stripped from these roots and all their branches in the excavated zone to see if they were colonized by A. mellea.

RESULTS

Intensive Root Observations

Nonwoody roots.--There were no significant differences in mean number of first-order nonwoody roots among trees scarcely or heavily infested with scale or infected by N. coccinea var. faginata. All trees averaged 26±2 first-order nonwoody roots per 60 cm of length. However, trees infected with Nectria had substantially (P=.05) fewer 4th-order nonwoody roots (Table 1). Two of the five trees infected by Nectria also had a substantially higher than average percentage of dead 4th-order roots, 18 percent versus 5 to 8 percent.

Table 1.--Mean number of living and dead and percent dead 4th-order nonwoody roots on scale-infested and Nectria-infected beech trees.

Tree category	Living	Dead	% Dead
Scale-infested trees			
Zero to trace (control)	599±57[a]	29±5	5±1
Heavy to very heavy	674±35	45±8	7±1
Nectria-infected trees	364±34[b]	32±17	8±4

[a]Mean of five trees for total number of 4th-order roots on 36 nonwoody roots per tree (3 nonwoody roots per 3 lateral roots per 4 buttress roots) ± standard error.

[b]Significantly lower than other two averages for living roots (P=0.05).

Armillaria mellea colonization.--No evidence of colonization by A. mellea was found on roots of trees with zero to trace or heavy scale. The lack of colonization was not because the fungus was absent or scarce; most of their woody roots had moderate to high densities of rhizomorphs on their surfaces. Occasionally a rhizomorph was found on a nonwoody branch.

A. mellea occurred on roots of two of the five trees infected by N. coccinea var. faginata. On one tree a buttress root and all but one of the branch roots were colonized by the fungus. On the other tree, lateral branch roots on three of the four buttress roots were colonized by the fungus. These two trees had been extensively colonized by Nectria and had dead bark on greater than 50 percent of their circumferences from midcrown down to within 2 meters of the root-stem base. Conks of the decay fungi Phellinus ignarius (Fr.) Quel. and Fomes fomentarious (L. ex Fr.) Kickx. were growing on the bark. Fifty percent of the trees' crowns were dead.

The three trees whose roots were not colonized by A. mellea also had necrotic stem bark. However, the necrotic streaks extended only to midbole, were less than 50 percent of the circumference of the bole, and appeared to be more recent necrosis. No symptoms or signs of decay were visible.

Root starch.--Seven of the 10 trees infested with either trace or heavy scale had high starch content in the roots and three trees had moderate root starch. The level of scale infestation had no effect (Table 2). In contrast, one of the five trees infected by N. coccinea var. faginata had moderate starch; the others had less or were starch-depleted. The two trees with roots that were colonized by A. mellea had low starch.

Table 2.--Numbers of trees with various root starch levels in relation to scale infestation and Nectria infection.

Tree category	Starch level[a]			
	High	Moderate	Low	Depleted
Scale: zero to trace	3	2	0	0
Scale: heavy	4	1	0	0
Nectria-infected	0	1	2[b]	2

[a]Estimated by histochemical technique (Wargo 1975).

[b]Both trees had roots colonized by A. mellea.

Extensive root observations

In all areas A. mellea had colonized roots on 50 of 78 trees examined, 18 of the 23 trees that had died recently and 32 of the 55 trees that were dying (Table 3). However, the fungus had totally colonized the root system on only four trees, two dead and two dying (Table 3). On these four trees the whole crown appeared to have died at once. Freshly wilted foliage or remnants of necrotic leaves were present on all branches and there was no evidence of previous upper-crown dieback.

Not all trees that appeared to have died suddenly and totally were colonized by A. mellea. In New York there was one such tree in each area. In Pennsylvania there were nine trees that were not colonized by A. mellea (Table 3). These trees, which were heavily colonized by beech scale, had apparently leafed out in the spring and then wilted. Bark necrosis occurred on the complete circumference of the trees down to within 0.5 meters of the root-stem base. No perithecia of N. coccinea var. faginata were visible on the bark of these trees but there were many tarry spots that indicated Nectria infection. The ratio of colonized to uncolonized trees in the Pennsylvania area was 0.6, much lower than the 3.1 and 5.0 for the two New York areas. This area in Pennsylvania had abnormally low precipitation that spring and summer (1981) and these trees were probably also stressed by drought.

Table 3.--Numbers of beech trees with crowns that died slowly over several seasons or rapidly within one season and with roots that were or were not colonized by Armillaria mellea.

		Numbers of recently dead or dying beech trees					
		Colonized by A. mellea			Not colonized by A. mellea		
Area	Crown death	dead	dying	total	dead	dying	total
Northeastern New York	slow	4	14	18	1	2	3
	rapid	2[a]	0	2	0	1	1
	Total	6	14	20	1	3	4
North-central New York	slow	10	7	17	0	5	5
	rapid	0	2[a]	2	0	1	1
	Total	10	9	19	0	6	6
Pennsylvania	slow	2	9	11	0	9	9
	rapid	0	0	0	4	5	9
	Total	2	9	11	4	14	18
All Areas	slow	16	30	46	1	16	17
	rapid	2	2	4	4	7	11
	Total	18	32	50	5	23	28

[a]Complete root system colonized by A. mellea.

The crowns of most trees that were colonized by A. mellea appeared to have died progressively from the top down. Upper crown branches had no leaves, twigs, or small branches on them, the bark was sloughing off branches and portions of the main stem, and on some trees fruiting bodies of the decay fungi F. fomentarius and P. ignarius were present on the main stem. The lower crowns had either chlorotic living or recently dead foliage and buds on the branches. On these trees A. mellea was always confined to roots associated with the oldest bark necrosis that resulted from colonization of the stem bark by N. coccinea var. faginata.

On some trees where necrosis of the stem bark was recent (bark dead but hard, tight, and intact), A. mellea was not present on roots associated with the dead streak. On other trees with recent stem necrosis, the fungus was just beginning to colonize the roots associated with the dead streak. Patches of mycelial fans occurred in the inner bark or cambial zone. On other trees with recent stem necrosis, some roots associated with the dead streak were entirely colonized by A. mellea. On some trees A. mellea was decaying roots associated with the oldest stem necrosis (bark soft, not intact, wood decaying); it had colonized the cambial zone tissues of roots associated with more recent stem necrosis, and was just invading the cambial zone tissues of roots associated with the most recent stem necrosis. This pattern was typical of the trees that had died recently. The fungus appeared to colonize these new root tissues from both rhizomorphs on the newly affected roots and mycelium from the previously colonized tissues. A. mellea had not colonized roots that were not associated with necrotic stem bark. These patterns were similar in New York and Pennsylvania.

A. mellea had also colonized roots associated with dead sections of the stems on the trees that had dead portions in the upper crowns and apparently healthy lower crowns. However, on these trees callus tissue had developed along the edges of root tissues colonized by A. mellea and no additional tissues were invaded. Colonization of the stem bark by N. coccinea var. faginata had also stabilized. Scale populations were scarce to light. In three of the five trees both roots and stem were in the advanced stages of decay.

DISCUSSION

Armillaria mellea was not a very aggressive colonizer of beech trees that were infested by beech scale, C. fagisuga and infected by N. coccinea var. faginata in four stands in New York in the "killing front" and in two stands in Pennsylvania in the "advancing front". Although A. mellea had colonized roots of dead and dying trees that were infected by Nectria, on most trees the root fungus had colonized less than 50 percent of the buttress roots and was restricted to roots associated with stem necrosis caused by Nectria colonization. The fungus was not observed colonizing adjacent roots in advance of the circumferential margins of stem necrosis. Most trees died because they were first girdled above ground by N. coccinea var. faginata, killing the stem bark, not because A. mellea colonized and killed the roots.

The sequence and timing of stem necrosis caused by N. coccinea var. faginata and colonization of roots by A. mellea seems to be as follows: scale insects infest and N. coccinea var. faginata colonizes and kills stem bark (Fig. 1a); the area of bark necrosis (and therefore the portion of the root system affected) is determined by the scale population density and area of infestation (Perrin 1980); a portion of the root system is affected and the roots may be colonized by A. mellea (Fig. 1b); if no additional stem bark necrosis occurs, the tree compartmentalizes the necrotic areas and the affected tissues decay (Fig. 1c); if additional stem bark necrosis occurs (Fig. 1d), additional roots are affected and may be subsequently colonized by A. mellea (Fig. 1e). Stem and root necrosis could develop quite rapidly if scale infestation were heavy for extended periods and large areas of stem bark were infected by Nectria.

The limited colonization of the root systems by A. mellea in beech stands stressed by beech bark disease is in contrast to colonization of northern hardwoods and oaks stressed by defoliation where the fungus aggressively attacks whole root systems and kills trees (Houston and Kuntz 1964, Wargo and Houston 1974, Wargo 1977). Observations on the fine roots and starch content of the roots in this study suggest that this difference occurs because the beech scale itself has a minimal effect on root growth and the effects of Nectria's killing the stem bark are confined to those roots associated with that portion of the tree. Defoliation, however, has a general debilitating effect on the whole root system.

The combination of defoliation by insects such as the saddled prominent, Heterocampa guttivita, and beech bark disease could be disastrous. Beech trees infected by Nectria could be "preinoculated" with A. mellea and therefore predisposed to rapid colonization by the root fungus when defoliation occurs. In this situation A. mellea could cause significant rapid mortality. In studies of A. mellea on oak, mortality after heavy defoliation was higher in areas that had a history of defoliation (Wargo 1981a). Excavation of surviving trees that were defoliated revealed that A. mellea was established in the roots and these trees were predisposed to subsequent colonization by A. mellea when the next defoliation occurred (Wargo 1977).

The lack of aggressiveness by A. mellea could also be due to the strain of the root fungus. Several clones and biological species of A. mellea have been identified (Anderson and Ulrich 1978) and they may differ in their ability to infect trees (Shaw 1978). Isolates from northern hardwoods are different from isolates from oak in their ability to metabolize tannins and related phenols (Wargo 1980b, 1981b). Beech is related to oak and may be chemically similar and therefore less susceptible to isolates that evolved in predominantly birch-maple stands.

Houston (1974) reported that some trees affected by beech bark disease were colonized by A. mellea and these trees died rapidly. My study shows that the majority of trees affected by beech bark disease are colonized to some extent by A. mellea but only a few are colonized enough that the fungus can be considered a major factor in the trees' death. The fungus colonizes the roots of most trees after the stem tissues have died and begun deteriorating, late in the decline of the tree when the tree is already beyond salvage. Houston (1974 and personal communication) compared rapidly killed trees with living trees that had symptoms of beech bark disease and excavated only the root collar area. He may have looked at trees before their colonization by the root fungus or perhaps missed the fungus by not looking farther out on the roots.

A. mellea does not seem to accelerate mortality in stands affected by beech bark disease except in a few trees. Most trees attacked by N. coccinea var. faginata and by A. mellea do not appear to die faster than those attacked by Nectria alone. It seems that A. mellea will not contribute significantly to the management problem associated with rapid tree deterioration in stands where beech bark disease is occurring.

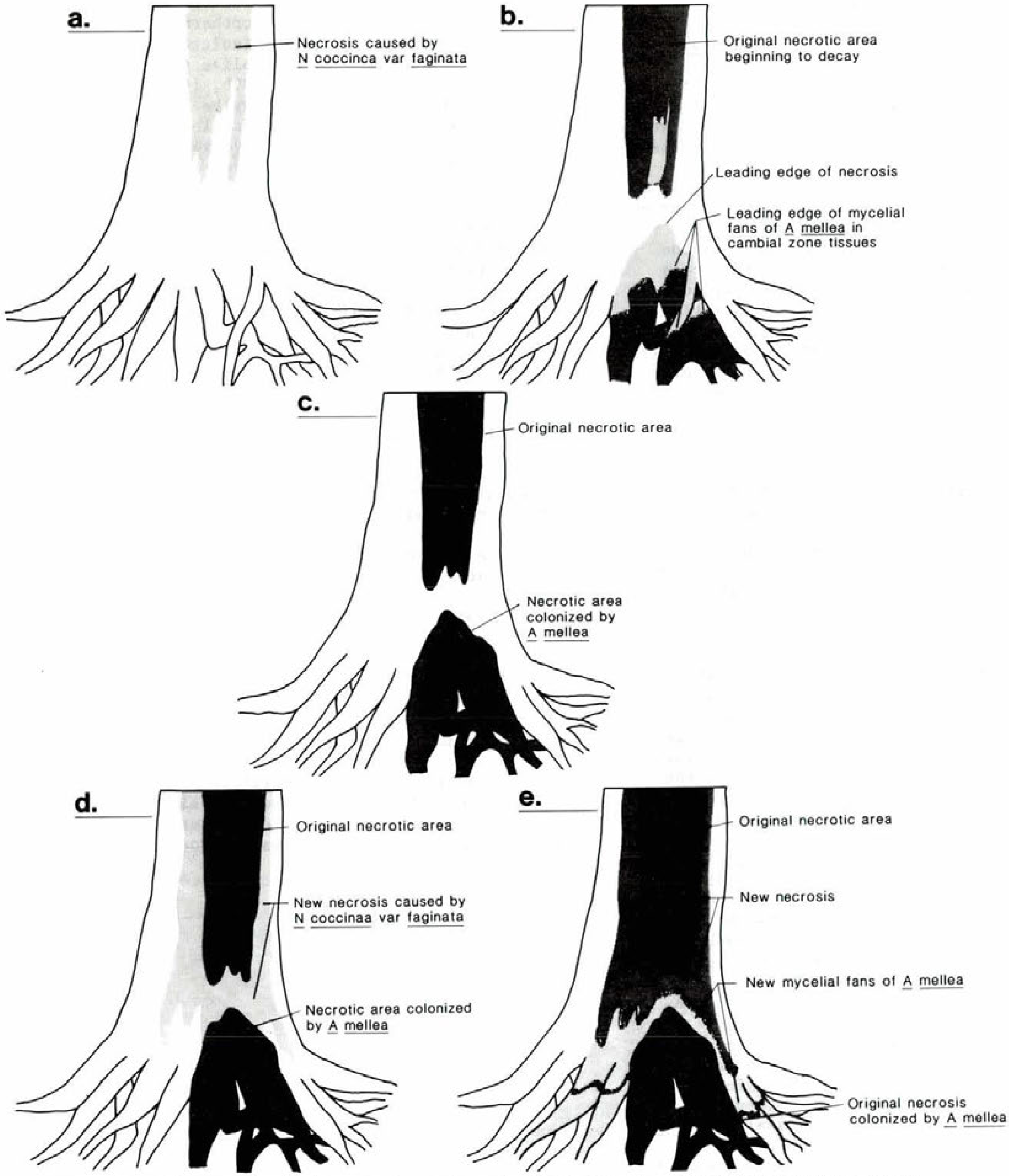

Figure 1.--Diagram of the lower stem and root-stem base of a beech tree illustrating the timing and pattern of stem colonization and subsequent necrosis caused by Nectria coccinea var. faginata and corresponding colonization of the roots by Armillaria mellea. *a*. Initial stem necrosis caused by N. coccinea var. faginata. *b*. Necrotic area of stem tissue beginning to decay; corresponding section of the root system colonized and killed by A. mellea. *c*. Necrotic area on stem '. advanced stages of decay; necrotic area in roots completely colonized by A. mellea and beginning to decay. *d*. New stem necrosis caused by N. coccinea var. faginata adjacent to original necrosis. *e*. Invasion by A. mellea of roots corresponding to area of new stem necrosis.

SUMMARY

Excavation of beech trees in stands affected by beech bark disease in New York in the "killing front" and in Pennsylvania in the "advancing front" revealed that infestation by the scale had little effect on the root system. Only trees infected by Nectria coccinea var. faginata showed any effect on the root system. They had fewer 4th order nonwoody branch roots and less starch than trees only infested by the beech scale, Cryptococcus fagisuga. Trees infected by Nectria were also the only ones with roots that were colonized by Armillaria mellea. The fungus was found on the majority of trees and was consistently found on roots associated circumferentially with areas of stem bark necrosis caused by Nectria. Complete colonization of the root system by A. mellea on dying trees occurred infrequently and occurred on trees that appeared to have died during a single growing season. The majority of trees were partially colonized, or colonized in stages associated with episodes of stem bark necrosis and crown death. The crowns of these trees appeared to have died in stages over several growing seasons. The roots were colonized by A. mellea after stem bark necrosis. A. mellea did not seem to accelerate mortality in these stands affected by beech bark disease.

RÉSUMÉ

L'excavation de hêtres dans des peuplements situés dans la "zone d'avance meurtrière" de la maladie dans l'Etat de New-York et dans la "zone d'avance primaire" en Pennsylvanie, a révélé que l'infestation par la cochenille avait peu d'effet sur le système radiculaire. Seuls les arbres infectés par le *N. coccinea* var. *faginata* montraient quelques effets sur le système radiculaire. Ils avaient moins de radicelles du 4ème ordre de ramification et non lignifiés, et moins d'amidon que les arbres infestés seulement par la cochenille du hêtre, le *Cryptococcus fagisuga*. Les arbres infectés par le *Nectria* étaient les seuls possédant des recines colonisées par l'*Armillaria mellea*. Le champignon se retrouvait sur la majorité des arbres et était constamment présent sur les racines associées (circonférentiellement) avec des parties nécrosées de l'écorce du tronc causées par le *Nectria*. La colonisation complète du système radiculaire par *A. mellea* chez les arbres mourants était peu fréquente et survenait sur les arbres qui semblaient être morts à l'intérieur d'une saison de croissance seulement. La majorité des arbres étaient partiellement colonisés ou colonisés à différents stades selon les étapes de la nécrose de l'écorce du tronc et de la mortalité de la cime. Les cimes de ces arbres semblaient être mortes par étapes à l'intérieur de plusieurs saisons de croissance. La colonisation des racines par le *A. mellea* survenait après une nécrose de l'écorce du tronc. Le *A. mellea* n'a pas semblé accélérer la mortalité et de là la détérioration dans ces peuplements affectés par la maladie de l'écorce du hêtre.

ZUSAMMENFASSUNG

Ausgrabungen des Wurzelwerks von Buchen in Beständen, die von der Buchen-Rindennekrose befallen sind, ergaben, daß der Lausbefall sowohl im Bereich der "killing front" (New York) als auch im Bereich der "advancing front" (Pennsylvanien) nur geringe Auswirkungen auf das Wurzelsystem hat. Nur Bäume, die von Nectria coccinea var. faginata befallen waren, zeigten Wirkungen im Wurzelbereich. Sie wiesen weniger unverholzte Seitenwurzeln 4. Ordnung und einen geringeren Stärkegehalt auf als Buchen, die nur von Cryptococcus fagisuga befallen waren. Auch wiesen nur von Nectria befallene Bäume Wurzeln auf, die von Hallimasch besiedelt waren. Der Pilz war an den meisten Bäumen zu finden und zwar regelmäßig an den Wurzeln auf der Stammseite, wo auch Teile der Rinde von Nectria befallen waren. Eine völlige Besiedlung des Wurzelsystems absterbender Buchen kam nicht häufig vor und dann nur bei Bäumen, die offenbar innerhalb einer Vegetationsperiode abgestorben waren. Die meisten Bäume waren nur teilweise oder in Relation zu Rindennekrose und Absterben der Krone vom Hallimasch befallen. Die Kronen dieser Bäume schienen schrittweise, im Laufe mehrerer Vegetationsperioden, abgestorben zu sein. Die Besiedlung der Wurzeln durch A. mellea fand nach der Rindennekrose statt. Der Hallimasch scheint demnach das Absterben der Buchen und damit die Verschlechterung des Gesamtzustandes der von der Buchen-Rindennekrose betroffenen Bestände nicht zu beschleunigen.

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