FUNGAL SUCCESSION ON NEEDLES AND YOUNG TWIGS OF OLD-GROWTH DOUGLAS FIR [1]

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SUMMARY

The pattern of presence and abundance of fungi on needles and twigs of old-growth Douglas fir (*Pseudotsuga menziesii*) in the Oregon Cascades exhibits a well-defined successional sequence which was documented by counting thalli and fruiting bodies under a dissecting microscope. Detailed information on the distribution of fungi in this habitat suggests that their mode of nutrition has yet to be elucidated.

Because of their short life cycles and minimal requirements for living space fungi have often been the subject of successional studies; however, such studies have usually dealt with successions on dead material (Webster, 1956; Hudson and Webster, 1958; Kendrick and Burges, 1962; Macauley and Thrower, 1966) and less frequently with those associated with living plants. The leaves and twigs of evergreen plants in a seasonal temperate climate provide an ideal substrate on which to study fungal succession since leaves are produced at defined intervals and persist for many years; in a single year of observation 8–15 yr of sucession are observed.

MATERIALS AND METHODS

The principal study site is an old-growth Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] stand located at an elevation of 500 m in the H. J. Andrews Experimental Forest, Lane County, Oregon. A single living tree, rigged for nondestructive sampling by a team of climbers by the method outlined by Denison et al. (1972), was selected for detailed study. In addition, two smaller trees from an adjacent area clearcut in 1952 and a number of saplings 2–10 yr old were examined superficially to determine whether a significant difference existed between the fungal flora of old-growth and younger trees.

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Fig. 1. Microhabitats on a Douglas fir twig. 1. Sooty mold on young twig. 2. Node and bud scales. 3. *Massarina* on young bark. 4. Lower surface of needle. 5. Upper surface of needle.

Branchlets, defined for purposes of the study as material less than 4 cm in diam, were removed from the upper, middle, and lower canopy layers, the lower layer being defined as the interval between the lowest living branch and the point at which branches became regularly spaced, about 40 m above ground level. The uppermost branch was collected at the top of the climbing path, 59 m above the ground. Later the branches on this tree were numbered in conjunction with a study of tree biomass and we received material from branches 5 (24 m), 7 (26 m), 33 (47 m), and 61 (53 m).

Initially, the main axis of each of the branchlets received was selected for detailed study. This axis was divided into yearly increments, and, where needles were present, 20 of them were removed and mounted between glass microscope slides. The exclusive use of the main axis appeared to introduce a bias into the sampling, since the main axis is thicker than the laterals at a given age, so we subsequently divided all material on a branchlet into yearly increments and drew samples randomly from bags of uniform age material.

Needles and twigs were examined at 25 and 50 × magnification using a Leitz dissecting microscope, and all thalli visible and identifiable at this magnification were recorded. Doubtful specimens were mounted in lactophenol-cotton blue and examined under a compound microscope for

verification. Voucher specimens of fungi noted have been deposited in the Oregon State University Herbarium (OSC).

Upper and lower surfaces of needles and twigs, and twig nodes with their accompanying bud scales were treated as separate microhabitats (FIG. 1). Upper surfaces receive more light and water than lower surfaces, and stomata are confined to the underside of needles. Nodes and bud scales are highly resinous. Insects and insect damage were noted when they occurred; however, in the Andrews Forest insects appear to be rare on old-growth Douglas fir branchlets. Sooty-mold colonies were dispersed and plated on tap-water agar. Further attempts to survey fungi by cultural methods were abandoned when it was found that many of the common visible fungi would not grow on any media. This study did not attempt to document the numerous sterile hyphae, algae, and bacteria unrecognizable under a dissecting microscope. Rare organisms were scored for presence or absence; the most common organisms were rated according to cover or abundance classes.

A list of fungi occurring on younger trees, and the approximate age of the organ on which they occurred, was compiled, but no quantitative sampling was attempted.

RESULTS

Although Douglas fir twigs and needles are an exposed, harsh habitat for fungi, a surprising number of forms fruit there. Fungi which could be positively identified are listed in TABLE I; colonizers of dead material are omitted. The last seven taxa in the table were isolated repeatedly from sooty-mold colonies; young trees were not investigated.

NEEDLES

Needles of old-growth Douglas fir at this study site are generally free from obvious disease symptoms although they support a large number of fungi. The number of needles per centimeter of twig decreases to half its original value after 6 yr and few needles persist longer than 8 yr. On young plantation-grown Douglas fir the percentage of foliage less than 4 yr old is estimated at 68% (Silver, 1962) and on old-growth trees 41% (M. Sherwood and J. Perkins, unpublished data). Parasites of older needles would therefore be expected to have more effect on old-growth trees.

Atichia sp. and trace amounts of sterile crustose lichens are present on the upper surface of 5–8-yr-old needles. At lower elevations in the Willamette valley these organisms become much more abundant. *Schizothyrium* sp. (undescribed, according to E. Müller) appears on

TABLE I

FUNGI OCCURRING ON NEEDLES AND TWIGS OF OLD-GROWTH DOUGLAS FIR[a]

Fungus	Young trees					Old-growth trees				
	Needles		Twigs			Needles		Twigs		
	U	L	U	L	N	U	L	U	L	N
Epipolaeum pseudotsugae (Mill. & Bonar) Shoem.		X								
Phaeocryptopus gaeumanii (Rohde) Petr.		X					X			
Schizothyrium sp.		X					X			
Atichia sp.	X		X		X	X		X		X
Aureobasidium pullulans (de Bary) Arn.	X		X	X	X	X		X	X	X
Lophium sp.			X							
Scolecobonaria lithocarpi (Mill. & Bonar) Bat.			X							
Diaporthe pitya Sacc.			X	X						
Caliciopsis pseudotsugae Fitzp.			X	X						
Strigopodia batistae Hughes					X					
Teichosporina sp.					X					
Massarina cf. *corticola* (Fuckel) Holm			X					X		
Winteria caerulea (Ell. & Ev.) Berl. & Vogl.			X					X		
Metacapnodium sp.			X		X			X		X
Antennatula sp.			X	X	X			X	X	X
Bactrodesmium cf. *obliquum* Sutton			X	X				X	X	
Epicoccum purpurascens Ehrenb. ex Schlecht.			X	X				X	X	
Lecidea erratica Körb								X		
Cladosporium oxysporum Berk. & Curt.								X	X	
Cladosporium cladosporioides (Fresen.) de Vries								X	X	
Cladosporium herbarum (Pers.) Link								X	X	
Nigrospora sp.								X	X	
Ulocladium botrytis Preuss								X	X	
Hyalodendron sp.								X	X	
Cephalosporium sp.								X	X	

[a] U = upper surface; L = lower surface; N = nodes and bud scales.

the lower surface of needles after 2 yr. On older needles up to 100 pseudothecia of this minute loculoascomycete were encountered, and on some twigs 100% of the needles were infected. Intensity of infection did not increase predictably with age or canopy level; however, some age classes were more severely infected than others, and the 7- and 8-yr age classes were almost uninfected, suggesting that parasitized needles dropped off prematurely (FIG. 2). *Phaeocryptopus gaeumanii* occurred occasionally on trees of all ages. Needles 4 and 5 yr old were most commonly affected. *Epipolaeum pseudotsugae* caused a severe needle cast on young saplings but was absent on older trees.

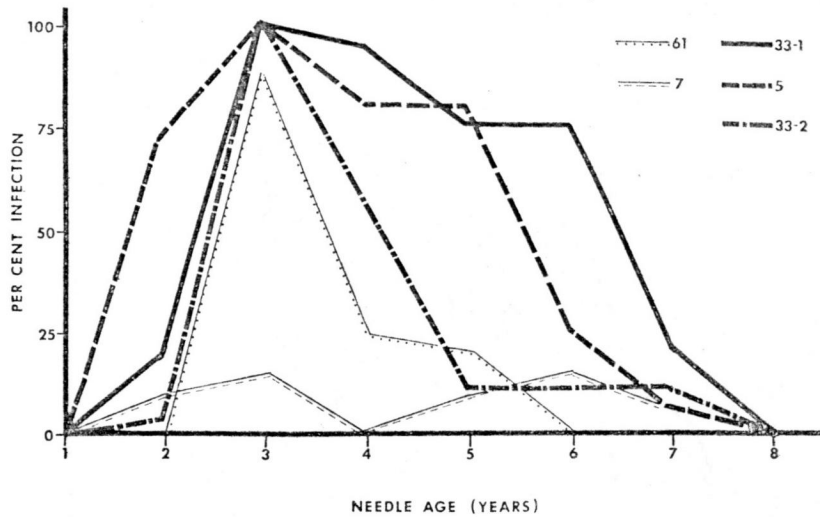Douglas fir trees do not mature a crop of cones every year. Since

Fig. 2. Per cent of needles infected with *Schizothyrium* sp. in four branch systems. Branchlet 33–1 arose near the trunk; 33–2 near the tip of branch system 33.

cones are shed the year after they are produced, the only cones available for study were those produced in the spring of 1972 and these were too young for successional observations.

TWIGS

Twigs remain smooth barked and photosynthetic until after the needles are shed. Thereafter the bark thickens and becomes sharply differentiated into an upper, lichenized zone and a lower zone which receives little moisture and is sparsely colonized by liverworts and sooty molds. Twig fungi occur in two distinct associations: the sooty molds (Capnodiaceae) and fungi that inhabit sooty-mold colonies, and parasitic bark-inhabiting loculoascomycetes. Both groups are eventually displaced by crustose lichens. Resin deposits at the nodes support distinctive fungi.

Sooty molds are most abundant on small-diameter twigs 3–8 yr old toward the upper canopy of older trees, but are present on trees of all ages. Hyphae of *Metacapnodium* and *Antennatula* appear in the second year and occasionally cover the entire twig. We did not observe ascocarps of either fungus. *Atichia* sp., *Aureobasidium pullulans*, and numerous algal cells (*Protococcus* sp. and *Trentepohlia* sp.) were frequently encountered in the association. Heavily colonized twigs showed no evidence of insect infestation and their position in the canopy renders
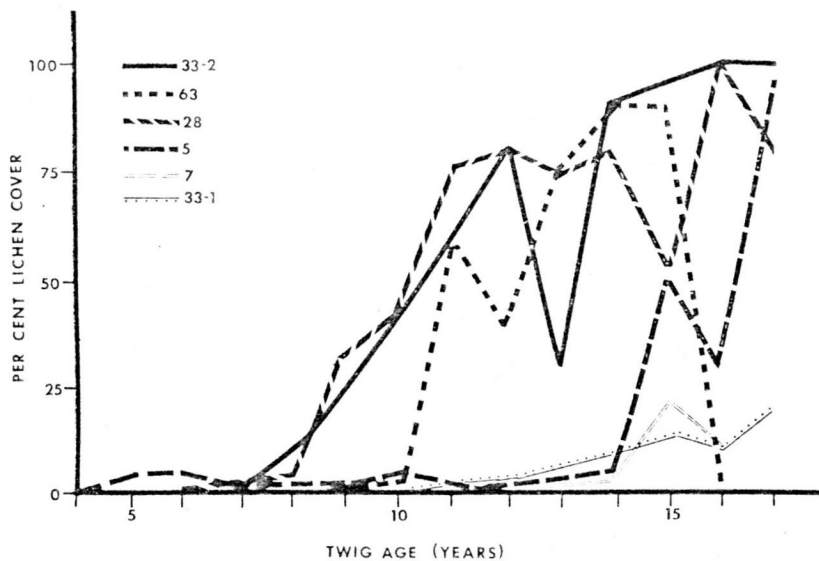
FIG. 3. Lichen cover on upper surfaces of twigs in four branch systems.

unlikely the hypothesis that insect exudates from other trees were a source of nutrients.

Strigopodia batistae is a characteristic inhabitant of resin. *Teichosporina* sp. occured on resinous bud scales of younger trees. *Scolecobonaria lithocarpi*, occasionally abundant on twigs of young saplings, does not occur on older trees. Old bud scales and twig epidermis are colonized by a thin network of *Aureobasidium* hyphae.

A number of parasitic loculoascomycetes inhabit living bark; their very diversity precluded adequate documentation when duplicate specimens could not be obtained. *Massarina* cf. *corticola*, the most abundant such fungus, occurs at all canopy levels on all but the youngest saplings. Twigs which are rapidly enlarging are more suceptible; hence, young trees, healthy branches, and main axes support large populations of *Massarina*. It occurs primarily on twigs 10–15 yr old, i.e., immediately after the needles have been shed. Less abundant but equally ubiquitous is *Winteria caerulea* which favors slightly younger twigs. A lichen tentatively identified as *Lecidea erratica* appeared after 3 yr and consistently occupies approximately 25% of the upper surface of twigs 5–20 yr old with its thin inconspicuous thallus. Apothecia were rare.

In the upper canopy, crustose lichen cover rose rapidly from trace amounts at year 8 to 50–60% by year 15 (FIG. 3). This sequence was

delayed in the lower canopy Hypophloedal crustose lichens grow underneath *Massarina*, *Winteria*, and *Lecidea*. Sooty molds and resin fungi persist at lower levels in cracks in older bark. Details of lichen succession on older branches are given by Pike et al. (1974).

DISCUSSION

The needles and twigs of Douglas fir support a large and diverse population of fungi which differs in several respects from that found by other authors on temperate trees. Healthy living leaves of herbs and deciduous trees rarely support sporulating fungi (Apinis, Chesters, and Taligoola, 1973) and have usually been surveyed for fungi by cultures and incubation. *Aureobasidium* and *Cladosporium* spp., seen frequently here, have been recorded on *Fagus* (Hogg and Hudson, 1966), *Pisum* (Dickinson, 1967), *Nothofagus* (Ruscoe, 1971) and *Acer pseudoplatanus* L. (Pugh and Buckley, 1971) and are probably nearly ubiquitous on plant surfaces. Since the present study was conducted in the summer and litter was not examined, fungi fruiting on senescent or recently cast needles, corresponding to group 1 in Webster's (1956) classification scheme, were not sampled.

Sooty molds dominated by members of the Capnodiaceae are more charactersitic of tropical than of temperate forests. Fraser (1936, 1937) concluded that Australian Capnodiaceae and Atichiaceae derived their nutrition from insect exudates. We found no evidence for this in the Andrews Forest. Resin, leachates, and algal exudates are possible candidates for a nutrient source. If these fungi derive their nutrition from leachates they may be important in forest mineral cycling.

The richness of the community in this restricted habitat suggests that, as in soil, biochemical differentiation among morphologically similar organisms and their production of antimicrobial substances could provide a promising source of antibiotics.

ACKNOWLEDGMENTS

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