EFFECTS OF LARCH DEFENSES ON XYLOPHAGOUS INSECT GUILDS

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INTRODUCTION

One of the best studies of a xylophage consortium is the case of larch insects by Isaev and Girs (1975). In their book, a basic theory was presented about host responses to xylophagous insects injury. According to their concept of "sliding resistance," different trunk-infesting insect species have different reactions to the tree's defenses and invade the tree successively depending on the stage of its decline or dieback. With regard to the general tree status, groups of invaders were identified by the authors: 1) primary species invading living trees whose resistance may increase back to the initial level; 2) secondary species colonizing living trees with fatally disturbed metabolism, and 3) necrophagous species living only in dead trees.

However, owing to its general nature, this classification cannot provide a detailed coverage of all the complexities arising when analyzing the ecological niche of xylophages. In particular, the potential increase in xylophage subcortical penetration rate was related mostly to the defense system of an individual tree without consideration of the environmental conditions (Sukachev 1967, Smagin et al. 1980, Polikarpov et al. 1986).

STAND FACTORS AFFECT XYLOPHAGES

Certain groups of forest types have differential stress resistance and pronounced peculiarities in composition and structure of their xylophagous insect complexes (Yanovsky 1987). Thus, analyzing entomofauna within the framework of forest type classifications allows examination of both the peculiarities of the interaction between host tree and insects and interspecific relationships between insects: within ecologically homogenous insect groups (i.e. xylophages or phyllophages), between different insect groups (e.g. between xylophages and phyllophages) and also between phytophages and entomophages. Specific habitat conditions, plant defensive responses, both composition and structure peculiarities of a given biocenosis, as well as the insect "aggressiveness" determine outbreak probability and insect dispersal. All the above factors influence the rate of decline of individual trees and the total stand, and, thus, indicate the level probability for epidemics by the invading xylophage species (Yanovsky and Korotkov 1984).

Deadwood load and distribution throughout the stand varies with forest type. So, food availability for sparse xylophagous insect populations and their dispersal patterns vary accordingly. At the same time, variations in the forest type response to the insect invasion and, consequently, tree dieback rate are responsible for the xylophage epidemic level.

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INTERACTIONS AMONG XYLOPHAGES

Important also is the detailed analysis of xylophage interspecific relationships, with special regard to the primary infesting species located within a microstation (tree). Isaev and Girs (1975) divided the insect species into two groups based on their potential to overcome host defenses, disregarding the insect population density. Now we know that the aggressiveness of some insects varies with their abundance. Within the primary trunk infesting insect species two groups can be identified: 1) xylophages capable of inhabiting the nonfatally declining trees, regardless of their population density, and 2) xylophages which can invade weakened trees only by means of severe, high density attacks. In the absence of severe stand damage, the first group dominates during the early stages of tree decline. These trees are inaccessible to the species of the second group so long as they remain at low population density.

In case of a nonfatal tree declines, i.e. after surface fires, the species of the first group dominate xylophage complexes. They provide the conditions required for the attack of the second insect group, particularly if population density of the latter is low. This results in a sharp increase in the population density of insects of the second group, which the allows them to independently inhabit resistant trees.

Burned Versus Defoliated Larch Forests

These conclusions are consistent with the results of a study of xylophage outbreaks in the larch forests of middle Siberia, affected by fires (burned areas) and the siberian moth, *Dendrolimus superans sibiricus* Tschetv. In these stands the beetle, *Tetropium gracillicorne* Rtt. and the larch buprestid, *Phaenops guttulata* Gebl. are representative of the primary insect species, capable of inhabiting non-fatally declining trees. On the other hand, the big larch bark beetle, *Ips subelongatus* Motsch., which is notorious for its violent population fluctuations, is incapable of invading trees with only slight metabolic disturbance unless it attacks en masse.

Observations on the invading insect species groups at the early stage of stand decline show in defoliated stands, that the non-fatally declining larch trees are extensively attacked by the buprestids and *Tetropium* beetles that can overcome the host defense system and inhabit the trees with weakly disturbed metabolism (Table 1). Therefore, immediately after hatching, the nutrient status in the phloem is sufficient for larval feeding. The phloem physiological properties responsible for the oxidation processes do not differ noticeably from those of the control (Table 2). However, the free carbohydrate concentration in the phloem, that is vitally important for protein biosynthesis, is insufficient for the larval feeding due to the tree's low photosynthesis level.

The bark beetles only inhabit the most weakened trees (Table 1 and 2). A few small populations of these insects were able to colonize trees with non-fatal metabolic disturbance, but the subsequent larval development was interrupted by pronounced resinosis (Isaev and Girs 1975). The bark beetle's ecological niche consists of slightly weakened larch trees with nonfatal metabolic disturbances. In this period a sharp increase in oxidation processes is observed, but enough carbohydrates are retained in the host phloem for the bark beetle larval feeding.

The rate of stand decline determines the specific composition of the xylophagous insect group. In the burned areas, where the stands are severely damaged by fires, the bark beetles dominate these groups immediately during the year of the fire (Table 1). It is noteworthy, that the trees infested with the bark beetles exhibit all the signs of total decline. The needles of these larches regenerating from dormant buds are pathological (too long and with water excess) and do not contribute much to tree recovery. But short-term physiological imbalance of trees does not allow bark beetle invasion. Under these conditions, hosts in early stages of decline are inhabited by buprestids. However, a lot of dead trees scattered throughout the burned area favor bark beetle buildups (Isaev and Girs 1975). For this

Table 1. Numbers of different xylophagous insects per sq dm of trunk in burned and defoliated larch stands over time

Years after xylophage outbreaks	Mode of tree decline	Attacked part of trunk	Insect population density[1]		
			Phaenops guttulata	*Tetropium gracillicorne*	*Ips subelongatus*
		Burned area			
First	Fatal	Base	0.06	0.14	0.36
		Middle	0.02	-	0.86
		Top	-	-	1.04
Second	Fatal	Base	-	0.09	1.09
		Middle	0.01	-	1.29
		Top	0.07	-	0.41
Third	Nonfatal	Base	-	-	3.78
		Moth defoliated area			
First	Nonfatal	Base	1.97	2.04	-
		Middle	1.85	1.04	-
		Top	1.36	0.18	-
Second	Fatal	Base	1.97	1.18	0.29
		Middle	2.39	0.15	0.25
		Top	1.77	0.05	0.05
Third	Fatal	Base	0.42	0.45	2.00
		Middle	0.63	0.52	1.52
		Top	0.25	-	0.22
Fourth	Nonfatal	Base	-	-	2.80

[1]Number of larvae (*Tetropium* beetles and buprestids) or galleries (bark beetles) per 1 sq decimeter of trunk.

reason, at the maximum xylophage population level (the second year after outbreak initiation) the primary insect group consists only of this one species (Table 1).

Trunk Temperature Effects

The bark beetle outbreaks are also likely to occur in the stands previously damaged by the phyllophagous insects, but in this case the bark beetles are competitively displaced by the buprestids and *Tetropium* beetles. Invasion and spread of buprestids in the moth-affected larch forests is retarded by the fact that the adults lay eggs on one and the same trunk part. Usually, the eggs are concentrated on the most weakened trunk part, arranged in strips on the southern side where phloem decline is facilitated by warming (Table 3). (See also Bombosch, this volume.)

Increase in phloem surface temperature stimulates the general metabolic activity, which, in case of unstable metabolism, leads to the increase in oxidation and hydrolysis, protein decomposition, and

Table 2. Variations in tree phloem properties associated with invasion by various xylophagous species expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

State of insect colonization	Phloem property: Moisture content (% fwt) AV	%	Respiration rate (mg CO_2/g) AV	%	Reducing capability (ml 0.01 N J/g) AV	%	Total sol. carbohydrate (% dwt) AV	%	Starch (% dwt) AV	%
					Phaenops guttulata and *Tetropium gracillicorne*					
Preinvasion	63.6	112	0.40	95	5.2	100	5.2	85	5.8	85
Eggs	61.4	115	0.51	100	6.6	143	5.5	125	4.8	60
Eclosion	63.4	106	0.58	232	4.4	100	6.6	129	4.9	45
Larvae in phloem	31.5	58	0.25	61	1.1	24	2.8	42	4.2	24
					Ips subelongatus					
Oviposition	60.5	102	0.84	162	4.0	78	2.2	43	2.5	35

Table 3. Variation in phloem properties on the north and south sides of infested trunks expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

Side of trunk	Phloem properties: Temperature in day time (°C)	Moisture content (% fwt) AV	%	Total sol. carbohydrate (% dwt) AV	%	Starch (% dwt) AV	%
North (shaded side)	21.9	53.8	80	7.5	59	3.2	32
South (sunny side)	25.7	48.6	73	3.0	24	1.1	11

decreases in tree defenses. The net result is that host phloem nutrient status is maintained high enough for the buprestid larval development. The phloem on the northern trunk part is wetter and richer in carbohydrates and starch. Here the insect penetration is time-delayed. Trees in similar conditions that fortuitously go uncolonized renew their needle next year and do not thereafter usually suffer from insect attacks. In trees with minimally disturbed metabolism, early subcortical penetration by the larch buprestids and *Tetropium* beetles is considerably interrupted by defensive biochemical and anatomical responses. The first instar larvae attempting to inhabit the phloem and adjacent wood layer are affected by a pronounced resinosis, followed by encapsulation of the larval galleries by the corked phloem cells. (See Herms and Mattson, this volume.) As the larvae grow in size their capsules grow longer and are oriented along the trunk (total length is 0.5 to 0.7 cm). The capsule cavities are filled with resinous woody frass. This slow down the larval development rate, and increases mortality of the larvae in this period of time is up to 70 percent. The period of development of encapsulated buprestids and *Tetropium* larvae is considerably long. If the tree was inhabited late in summer, the larvae are expected to come out of the capsules in June next year. By this time the larvae are 2 to 3 mm long and their most rapid development is observed in July (Table 4). Doubtless, the larval development is most rapid on the warmest (southern) side of the trunk. Here, the larval galleries are wide and meandering as can be seen from the gallery length and area measurements (Table 4). Quite in contrast, on the northern side of the host tree the larval galleries are narrower and run straight up and down.

Due to this vertical direction of the larval galleries, the resin channels on the shaded side of the host plant are less damaged and, therefore, the larval mortality from resinosis is low. After being attacked by the *Tetropium* and buprestid beetles, the target trees exhibit a gradual decrease in resistance induced by the larval development. During the colonizing period and while larvae are encapsulated, the weakened trees do not differ greatly from the healthy ones in their physiological properties (Table 2). After this time the tree decline is obvious from the decrease in crown assimilation capability caused by the declining needle biomass followed by decreases in the phloem carbohydrate. The host plants show the first signs of decline by the time the larval emergence from capsules is over. This can be attributed to the general decrease in host viability manifested by reduced resin flow from the phloem resin channels. This, in turn, allows the larvae to extensively locate the intact zones of the phloem. On the other hand, the phloem destruction caused by the larval galleries leads to wound hyperoxidation which is evident from a sudden increase in respiratory rate, decrease in reduction capability, and gradual exhaustion of assimilant inflow which leads to decrease in carbohydrate concentration. These trees become attractive for the bark beetles. During the period of the young larval feeding, the host phloem suffers from a considerable water shortage.

Table 4. Development of larch buprestid larvae

Development variables	Side of trunk	Date of observation in July						
		4	8	14	17	22	27	31
Length of larvae (mm)	South	5.2	0.7	9.3	12.0	12.7	18.0	21.3
	North	3.8	4.2	4.2	4.7	7.5	9.0	9.0
Length of gallery (cm)	South	1.9	2.9	3.6	4.3	4.5	-*	-*
	North	0.9	1.4	1.5	2.1	2.8	2.8	4.6
Gallery area (cm^2)	South	0.51	1.12	1.99	2.21	3.21	-*	-*
	North	0.17	0.18	0.35	0.67	0.79	0.80	1.47

*Galleries join, making individual measurements impossible

Table 5. Variation in the larch phloem parameters in relation to bark beetle invasion expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

State of bark beetle colonization	Phloem property									
	Moisture content (% fwt)		Respiration rate (mg CO_2/g)		Reducing capability (ml 0.01 N J/g)		Total sol. carbohydrate (% dwt)		Starch (% dwt)	
	AV	%	AV	%	AV	%	AV	%	AV	%
Initial attack	62.5	104	0.40	91	3.8	80	2.2	43	4.9	76
Oviposition	58.4	99	1.08	179	4.2	75	2.4	38	5.2	66
Eggs and larvae	44.1	75	0.52	210	3.0	47	2.1	28	3.7	21
Larvae	50.7	88	0.67	110	5.1	78	2.3	30	3.7	21
Larvae and pupae	42.0	77	0.30	56	1.1	27	2.8	20	3.8	22
Larvae to callow adults	35.0	62	0.32	74	0.6	14	0.3	3	0	0

The buprestids and the *Tetropium* beetles weaken the tree to the level suitable for the bark beetle survival. Distinguished by its high reproductive potential, that is being capable to produce much more generations per unit time in comparison with other insects, the bark beetle populations rapidly grow, competitively displace the buprestid and *Tetropium* beetles and become the dominant consumer. A significant difference between the bark beetles and other insects of interest lies in the way bark beetles injure the trees at high population density level. Symptoms of the declining host resistance become visible in the period of the bark beetle subcortical penetration and gallery construction. This period is characterized by the phloem hyperoxidation and total carbohydrate decline (Table 5). By the time the galleries are made the phloem tissues appear to be significantly damaged by the bark beetles. Crown isolation from the root system as well as the decrease of downward assimilant flow contribute to the host gradual dieback. During construction of larval galleries, the phloem moisture content, and the carbohydrate and starch concentration are reduced and the phloem turns brown owing to irreversible oxidation of many tissues (Table 5). The adult bark beetles are very capable of overcoming the host defense system, hence, they are largely responsible for the tree's defensive decline. A sharp decrease in the host defenses is observed during the mass larval hatching. At this stage of development the larval mortality is no more than 30 percent. Now the larval growth is no longer interrupted by the phloem defensive response. However, the phloem carbohydrate concentration remains comparatively high providing suitable conditions for the larval feeding and development.

It can be concluded that examination of xylophage group composition at the time of an outbreak allows one to predict the extent of decline both the individual tree and total stand. Sparse populations of the *Tetropium* and buprestid beetles located on resistant trees indicate that reduction of tree defenses below a critical level may allow bark beetle infestation to follow. On the other hand, the subcortical penetration of the low density bark beetle populations predict an ominous future for the stand.

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