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Green islands – predation not nutrition

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Summary. The existence of green islands around wood-ant nests in otherwise damaged birch forests has been explained by two alternative hypotheses: (1) predation by ants protects the trees against defoliators, and (2) the ants ameliorate tree vigor by concentrating soil nutrients. The size of green islands and the nitrogen content of the soil and foliage do not support the nutrition hypothesis. These data and general knowledge about the foraging strategy of wood ants are consistent with the predation hypothesis.

The hypotheses

White (1985) argues that green islands of mountain birches surrounding wood-ant nests in Northern Finland are not due to the ants' predation on defoliators during outbreaks as we have proposed (Laine and Niemelä 1980). According to White's explanation, the ants benefit the birches by concentrating soil nutrients in and around their nests. During outbreaks, birches in ant territories are relatively unstressed and make poor food for defoliating larvae, which therefore suffer from high mortality. These trees then remain as green islands.

An unambiguous test between White's hypothesis and ours would be to compare the survival of larvae on birches with experimentally manipulated nutrient availability and ant attendance. Having not yet done the experiment we, nevertheless, point out some observations in our study area and elsewhere that do not support White's reasoning. They concern three topics: the range under ants' fertilizing and predatory activity, the relationship between soil nutrients and leaf quality, and the foraging ecology of ants.

The range of ants' influence

We do not deny that wood ants may have local importance in bringing organic matter in their nests and excavating soil. There is a large literature on this subject (see Buckley 1982 for a review). The critical point in White's line of thought is whether a single ant nest is capable of affecting tree vigor as far as 20 m from the nest, which is the size of green islands (Fig. 2 in Laine and Niemelä 1980).

To our knowledge, there is no evidence that ants can do such large-scale manipulations of the soil. White based his assumptions on studies of tropical termites by Salick et al. (1983). This paper contains no information about the range of fertilizing effect, except that it is obvious in and just around the nest. In North America Beattie and Culver (1977) found that soil conditions were altered within 1.5 m of wood-ant nest mounds but not beyond. The results reviewed by Pętal (1978) imply similar ranges of soil modification by several temperate ant species.

Another possible mechanism with the same outcome would be the potential of trees for selective root growth. It is known that birches may have higher root densities in patches of decaying organic material (Laitakari 1935). But how far do the roots reach? We calculated the extent of birch root systems using Laitakari's data from 12 trees growing on sandy and morainic soils (which are the soil types in our study site). The longest root per tree averaged 5.6 m, while the maximum length observed for any root was 11.0 m. The area covered by the whole root system was no more than 37.1 m^2 on average. Thus, it seems unlikely that a tree growing at the edge of a green island could exploit whatever nutrients there were in the mound.

On the other hand, the extent of ants' predatory activity has been found to range from 8 to 60 m in a number of studies (Bruns 1958, Tilman 1978, Inoye and Taylor 1979, Wellenstein 1980). The radius of green islands (17–22 m according to Wellenstein and 15–20 m according to our results) falls well within these boundaries and exceeds the range of soil modification activity by the ants and the area of the root system. Therefore, we claim that the size of green islands is explained better by the predation than the nutrition hypothesis.

Soil nutrients and leaf quality

According to White's reasoning, birches in the green islands would have access to a concentrated source of nutrients, be more vigorous and offer less nitrogenous nutrients to herbivores than the stressed trees outside.

To assess directly this question we collected soil and foliage data in 1985. No clear trends could be observed in the soil except that potassium was slightly more abundant in ant nests (Table 1). What is important, is that nitrogen, the most restricting nutrient in the subarctic region (Haag 1974), was very low in every sample. Jakubczyk et al. (1972) also found that nitrogen content was unaffected by ants although potassium and phosphorus could be five times more abundant in their nests.

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Table 1. Range of nutrient contents (mg/l) of A 1 layer in the soil (31 July, 1985). Surroundings of two nests were analyzed in both areas

Area	Sample site	*n*	Ca	K	P	Mg	N
Damaged	Nest periphery	2	350–650	140–180	22–29	145–170	<10
	25 m from nest	3	500–550	100–130	13–44	110–200	<10
Healthy	Nest periphery	2	600	200	30–32	120–135	<10
	25 m from nest	3	500–550	120–170	32–45	85–130	<10

n = number of soil samples, N = nitrate nitrogen

Table 2. Nitrogen content (%) of birch leaves (31 July, 1985)

Area	Sample site	Foliar nitrogen content			
		mean	S.D.	*n*	t-value
Damaged	Nest periphery	1.87	0.25	4	0.775 N.S.
	25 m from nest	1.75	0.25	8	
Healthy	Nest periphery	2.00	0.08	4	0.052 N.S.
	25 m from nest	2.00	0.21	8	

n = number of trees studied

White expects that the trees growing near the ant nests would exhibit lower concentrations of nitrogen in the foliage. There was no significant difference in nitrogen content of leaves inside and outside green islands, nor in the corresponding samples from the healthy forest (Table 2). One may argue that total nitrogen content of leaves does not tell the whole story about tree vigor and availability of nitrogen to herbivores. Mattson's (1980) voluminous review implies, however, that total nitrogen is at least a good correlate of food quality.

Had we found differences in the nitrogen contents, a serious problem would still have remained about the relationship between soil nitrogen level and the herbivore resistance of the birch. Earlier results by our study group indicate that birches growing on poor soil support slower larval growth than trees on good soil (Haukioja et al. 1978). Larval success is negatively correlated with phenolic content (Haukioja et al. 1985b) and the phenolic content of leaves in trees on poor soil is higher than on good soil (Haukioja et al. 1985a). The reason for this is unclear. Perhaps trees growing on nutrient deficient soil cannot invest their carbon in growth and "excessive" carbon is stored as carbon-based defensive compounds like phenolics (Mattson 1980, Bryant et al. 1983).

Further, our experiments indicate that fertilization increases nitrogen content (but insignificantly) and significantly decreases the phenolic content of leaves (Tuomi et al. 1985). An obvious consequence is that increase of nitrogenous nutrients in the soil does not necessarily increase the resistance of the mountain birch, as White assumes. On the contrary, we believe that the opposite might be true.

Ant ecology

Knowledge about wood-ant foraging strategy does not support White's reasoning, either.

Finnegan (1974) among others has pointed out that ants differ from most nonsocial predators and parasites in exhibiting no numerical time lags behind increasing prey populations. This is because ants maintain high and stable densities during all phases of prey populations by switching rapidly from one prey type to another without becoming specialists to any (Horstmann 1972). When a given food source is even very locally abundant it is heavily preyed upon by ants. Predator satiation is not likely to occur since hunting motivation (of a forager) is uncoupled from hunger (of the brood) (Risch and Carroll 1982).

Another distinctive feature of ant colonies is that the number of foragers is relatively unaffected by temporal fluctuation in food supply (Risch and Carroll 1982). Adult ants rely for their energy demands on honeydew excreted continuously by tended aphids and other homopterans (Carroll and Janzen 1973). Adult ants can endure protein shortages by eating trophic eggs (Abbott 1978) and by cannibalizing the brood (Risch and Carroll 1982). Hence the colonies can survive and have a stable forager force over brief periods of scarcity of animal prey.

Our observations conform to this generalized picture. In 1979 we estimated that the mean size of mature colonies was 500,000 workers, a European average (Wellenstein 1973), although the numbers of the defoliating geometrid *Oporinia autumnata* were extremely low (Linnaluoto and Koponen 1980). What kind of protein food did the ants eat then? Another geometrid, *Entephria caesiata*, living on ground-layer vegetation had a peak year (Linnaluoto and Koponen 1980). Not surprisingly, 30% of prey biomass brought into the ant mounds in June consisted of its larvae. Also many other locally and temporally abundant invertebrates were caught in vast numbers. For example, 35% of animal food of one colony was psyllids when they were exceptionally numerous in mountain birches in the neighborhood for a few weeks. Midges were heavily preyed upon by all studied colonies when adults were emerging from aquatic systems. High ant populations seem to be possible in the subarctic, too, because ants are opportunistic predators and scavengers.

White was dissatisfied with the great variance in our direct estimates of herivore pressure on birch (Figs. 3 and 5 in Laine and Niemelä 1980). We noticed the amount of variation in our original paper and offered two possible reasons: differing ant visitation frequency and variation in birch antiherbivory tactics. Whether these reasons are correct or not, our main conclusion that herbivore pressure is lower in the green islands holds (Table 3).

These observations alone could, of course, be explained by the nutrition hypothesis as well. But there are many other studies with remarkably similar results, even about the same species or their close relatives. Recently Fowler and MacGarwin (1985) found experimentally that the free-living, leaf-tieing and leaf-mining guilds of *Betula pubescens*

Table 3. Herbivore pressure on birch in green islands and their surroundings (July 1979)

Measurement	Sample site	mean	S.D.	*n*	t-value
Intact leaves (%)	Green islands	59.75	5.74	4	2.553 $p<0.05$
	Surroundings	49.00	6.16	4	
Chewers/ 1000 leaves	Green islands	1.08	1.26	14	2.700 $p<0.05$
	Surroundings	2.47	1.69	26	

were reduced by the presence of *Formica lugubris*. More importantly, the degree of reduction diminished in this order and was inversely correlated with the ease of predation by ants. This finding is difficult to explain by differences in birch vigor.

When explaining the existence of green islands we never claimed, as White supposes, that ants alone are responsible for the topographical delimitation of birch damage. This is unreasonable since the lower boundary of the dead forest is visible also on those slopes where wood ants are absent. Candidates for the large-scale delimiting factors are winter climate (Tenow 1972) and differences in damage-induced reactions of the birch (Haukioja et al. 1983).

To summarize, we are convinced that predation, not fertilization, by wood ants is the main cause of reduced defoliation of birches in the green islands in our study area. The phenomenon is also known in other ecosystems including fertile Central European forests (Wellenstein 1980) and it applies also to systems where honeydew-producing homopterans are replaced by extrafloral nectaries (Tilman 1978). From the viewpoint of the plant, homopterans and nectaries have the same function: they guarantee evenly distributed patrolling of foraging ants in the foliage (May 1982). This may well be a viable defensive strategy of woody plants although it may never provide complete control of herbivore populations (Schemske 1980).

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