PATTERNS OF NUTRIENT UTILIZATION IN THE NEEDLE-FEEDING GUILD

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INTRODUCTION

It is well known that large differences in performance parameters such as growth rate, survival rate, or fecundity rate are found between various insect guilds, e.g. root feeders and sapsuckers (Slansky and Rodriguez 1987, Slansky and Scriber 1985). Within guilds and even within a given host plant, the variability of the plant material may also result in considerable differences in the performance parameters of insect larvae feeding on the plant (Whitham 1983, Jensen 1988).

Under constant laboratory conditions, variability in performance depends primarily on the nutrient and secondary compound content of the host plant material. Positive correlations between performance parameters and the carbohydrate, amino acid, or total nitrogen content can be found, while negative correlations have often been made between performance and the presence of phenolics, tannins, or alkaloids.

With a limited number of insect species such correlative analyses might be tested by using artificial diet studies. In such studies, however, it is extremely difficult to mimic the true composition of the various chemicals in the plant tissue. Another method is to study the fate of various biochemicals when ingested by a certain insect.

In the present investigation, the content of various biochemicals in the needles of conifers (*Pinus* and *Picea* species) was compared with the content of the same compounds in larval feces for a number of insect species within the needle-feeding guild. These species comprise conifer specialists within the Lepidoptera (*Bupalus pinarius*, *Dendrolimus pini*, *Panolis flammea*) and Hymenoptera (*Diprion pini*, *Neodiprion sertifer*, *Pristiphora abietina*, *Gilpinia hercyniae*, *Pachynematus scutellatus*, *Cephalcia abietina*) as well as the generalists, mainly Lepidoptera (*Orgya antiqua*, *Lymantria monacha*), known to use host plants other than the conifers.

EXPERIMENTAL METHODS

All insects were reared under standardized conditions, at 20°C and with 18 hr daylight, on whole branches cut from 40 to 60-year-old spruce and pine trees. First instar larvae were kept in groups, later instars singly. Most individuals were wild-captured or first generation laboratory-reared with the exception of *Diprion pini*, which came from the stock maintained at the University of Turku, Finland.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

Samples of needles were taken at the start and in the middle of the experimental period, and larval feces samples were collected 2 to 3 days after the needle samples were taken. Needles and feces were freeze-dried, ground, and stored in a desiccator in the dark at room temperature.

Polar compounds were extracted three times with methanol, 2 ml for 15 min at 65°C, each time with subsequent centrifugation, 5 min 2800 U/min at room temperature. The methanol extract was derivatized by oxime formation followed by silylation and applied to a gas chromatographic column (2m x 4mm) packed with SE52 on Chromosorb G. The internal standard method was used to determine the quantities derived from the chromatograms.

The total nitrogen content of the freeze-dried material was determined by means of the modified micro-Kjeldahl method.

RESULTS

Total Nitrogen

As expected, the total nitrogen content in conifer needles differs between old and young needles, highest values (ca. 4 percent dwt) being found in the newly flushed needles and decreasing as the needles grow old. Even at the start of the growing season, old needles have a very low ($\leq$ 1 percent dwt) nitrogen content.

Fig. 1 shows the concentration of nitrogen in spruce and pine needles compared with the concentration of nitrogen in the feces of several insect species. The consensus for all species and all types of food is that nitrogen utilization is low. The concentration of nitrogen in the feces is only slightly lower than that in the needles. Even in cases where the food has a content of about 1 percent, the concentration in the feces is close to the value in the needle. When the metabolic quotient is taken into account, the general utilization of nitrogen in these species is in the order of 45 to 55 percent.

Carbohydrates

In the present investigation, the concentrations of fructose, alpha- and beta-glucose, and sucrose were measured individually and the total amount of hexose-equivalents calculated as:

$$Chex = Fru + Glu + 2(Suc)$$

In pines few differences in carbohydrate concentrations were found between old and young needles, whereas among spruce somewhat higher concentrations were found in old than in the younger needles.

Fig. 2 shows the level of carbohydrates in the feces of all insect species investigated. The consensus for all species on all food resources is utilization is very high, 95 to 100 percent. Even when carbohydrate concentrations are very elevated, the utilization is almost complete. Carbohydrate values from insect consumption of male flowers are not included in the figure, but male flowers can have carbohydrate concentrations of 600 to 1,300 nmoles/g dwt, and in such cases the utilization is still 95 to 100 percent.

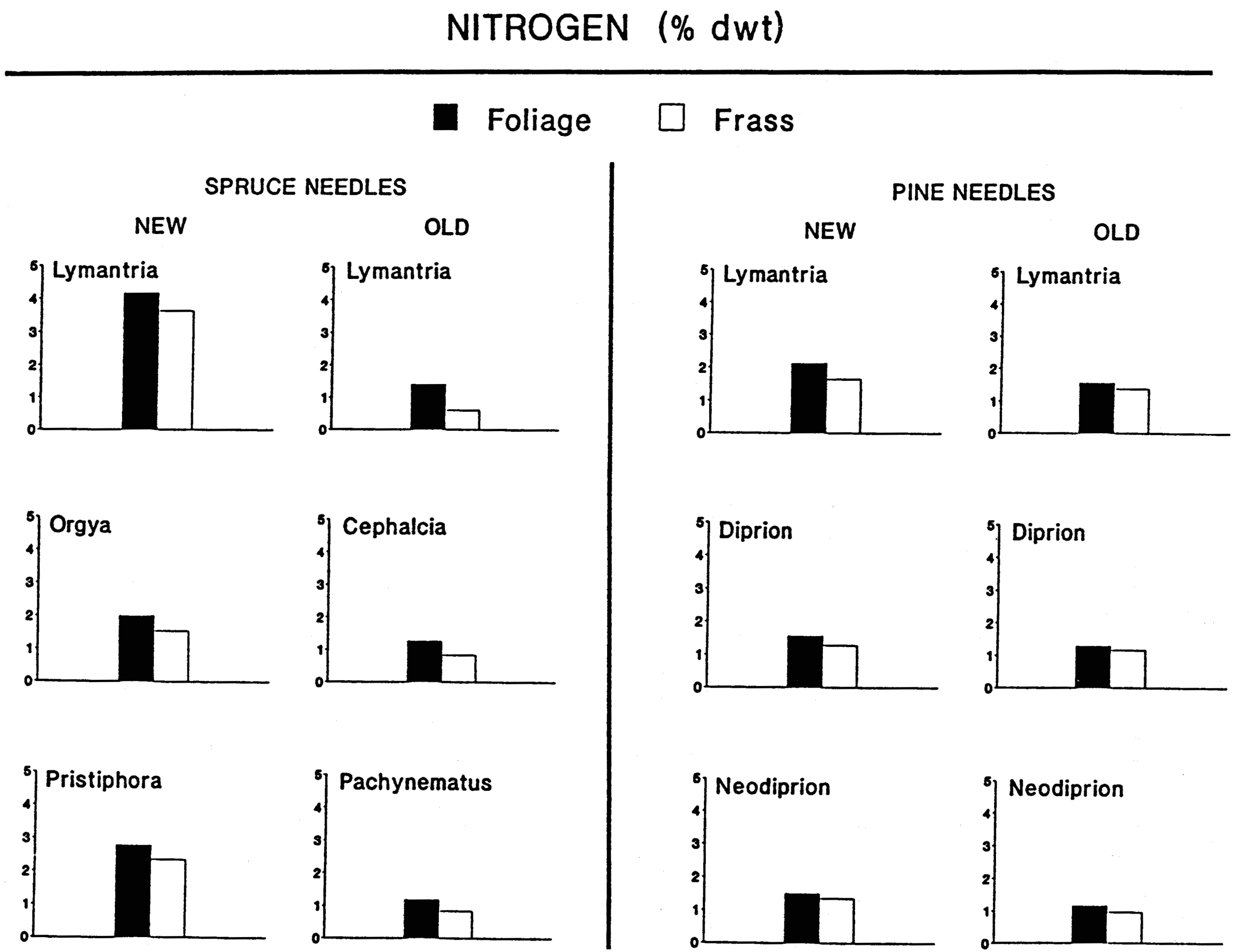

Figure 1. Concentrations of total nitrogen in new and old needles of spruce and pine, and in frass of insect herbivores.

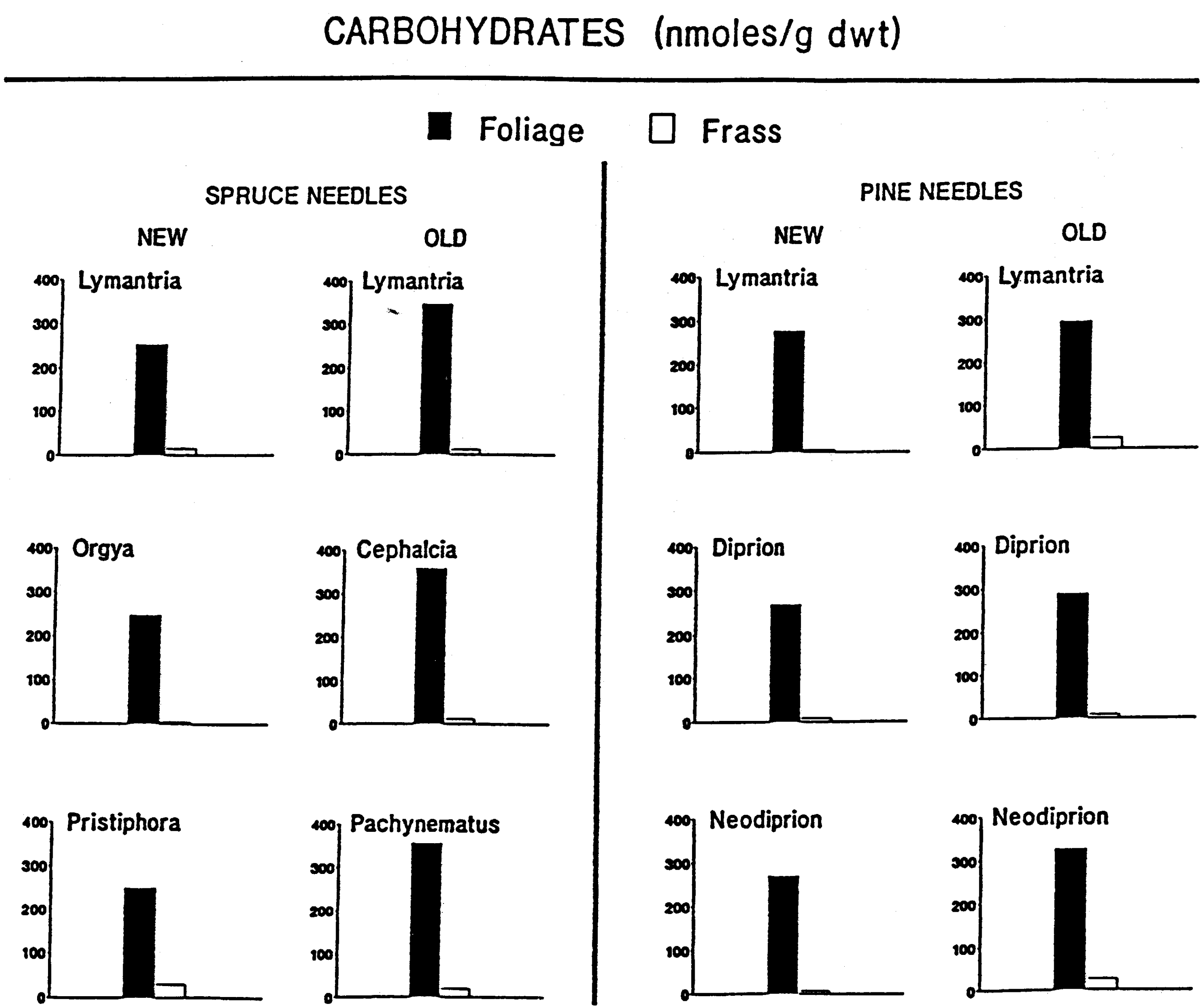

Figure 2. Concentrations of carbohydrates (hexose-equivalents of sucrose, fructose, and glucose) in new and old needles of spruce and pine, and in frass of insect herbivores.

Cyclites

Fig. 3 shows the concentrations of the conifer-specific cyclite (sugar alcohol), pinitol. Pinitol occurs in rather high concentrations, highest in the new needles. Male flowers also contain high amounts of pinitol. In most insect species there seems to be an almost complete utilization of this compound, although *Lymantria monacha* has a somewhat lower assimilation level/rate when eating old needles. When the concentration of pinitol in the food is very high, however, utilization seems to decrease.

The other cyclite, inositol, occurs in much lower concentrations (7 to 25 nmoles/g dwt) in the needles and in the male flowers. At low concentrations, all inositol is utilized, but at higher concentrations in the food, inositol can occur in concentrations of up to 17 nmoles/g dwt in *L. monacha* feces.

Phenolic Acids

Quinic acid is the low-molecular compound in conifer needles found in probably the most variable concentrations, ranging from 35 to 1,000 nmoles/g dwt. The high concentrations are found in newly flushed needles and in the male flowers of spruce and the lower concentrations in old pine needles.

Fig. 4 shows that the pattern of utilization of quinic acid is highly variable, depending on the insect/host plant system. The generalist *L. monacha* seems to tolerate this compound, quinic acid being present in the feces in concentrations equal to or even higher than in the needles. Taking the metabolic quotient into account, one may infer low or zero utilization.

The same pattern is found in the other generalist lepidopteran, *Orgya antiqua*, feeding on new spruce needles. The specialist pine lepidopterans, *Bupalus pinarius* and *Dendrolimus pini*, seem to follow the same pattern as well, and with them higher concentrations in the feces than in the old pine needles clearly indicate that quinic acid passes through the intestine unaltered.

In striking contrast, the specialist sawflies seem to utilize at least a part of the quinic acid when reared on their proper host. When *Diprion pini* and *Neodiprion sertifer* feed on old pine needles, concentrations of quinic acid in the feces are quite low. However, when these species are forced to feed on new needles with a higher content of quinic acid, the concentrations in the feces are higher, but still below the value in the needles.

The spruce specialist sawflies seem to follow this pattern. Although given higher concentrations of quinic acid in spruce needles, higher levels are also found in the feces, utilization seems to be similar.

Shikimic acid also shows a variable pattern between plant species and plant parts, highest values being found in old spruce needles and in *Pinus contorta* and lowest values in new spruce needles and male pine flowers (Fig. 5).

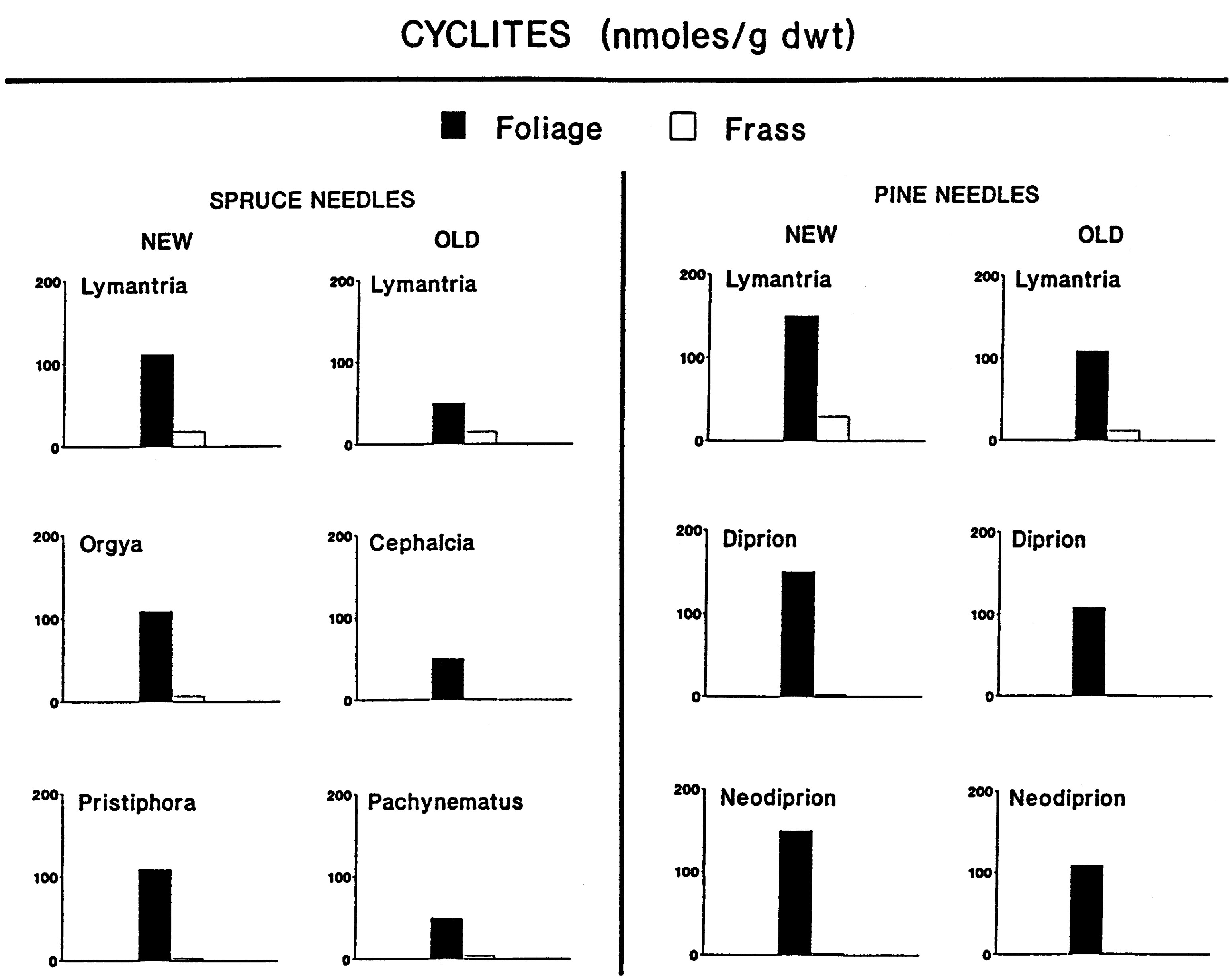

Figure 3. Concentrations of the cyclite, pinitol, in conifer needles and in herbivore frass.

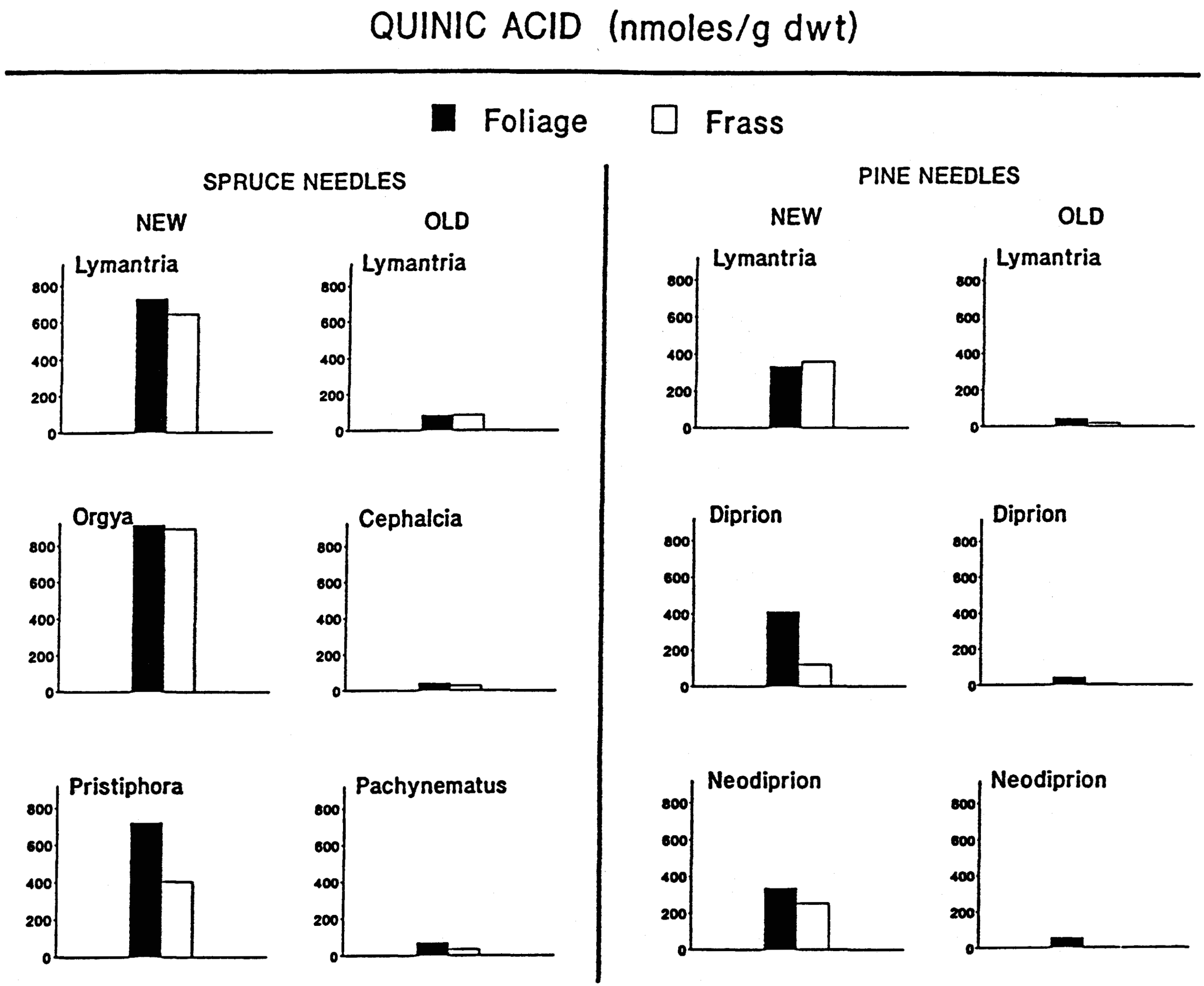

Figure 4. Concentrations of quinic acid in conifer needles and in herbivore frass.

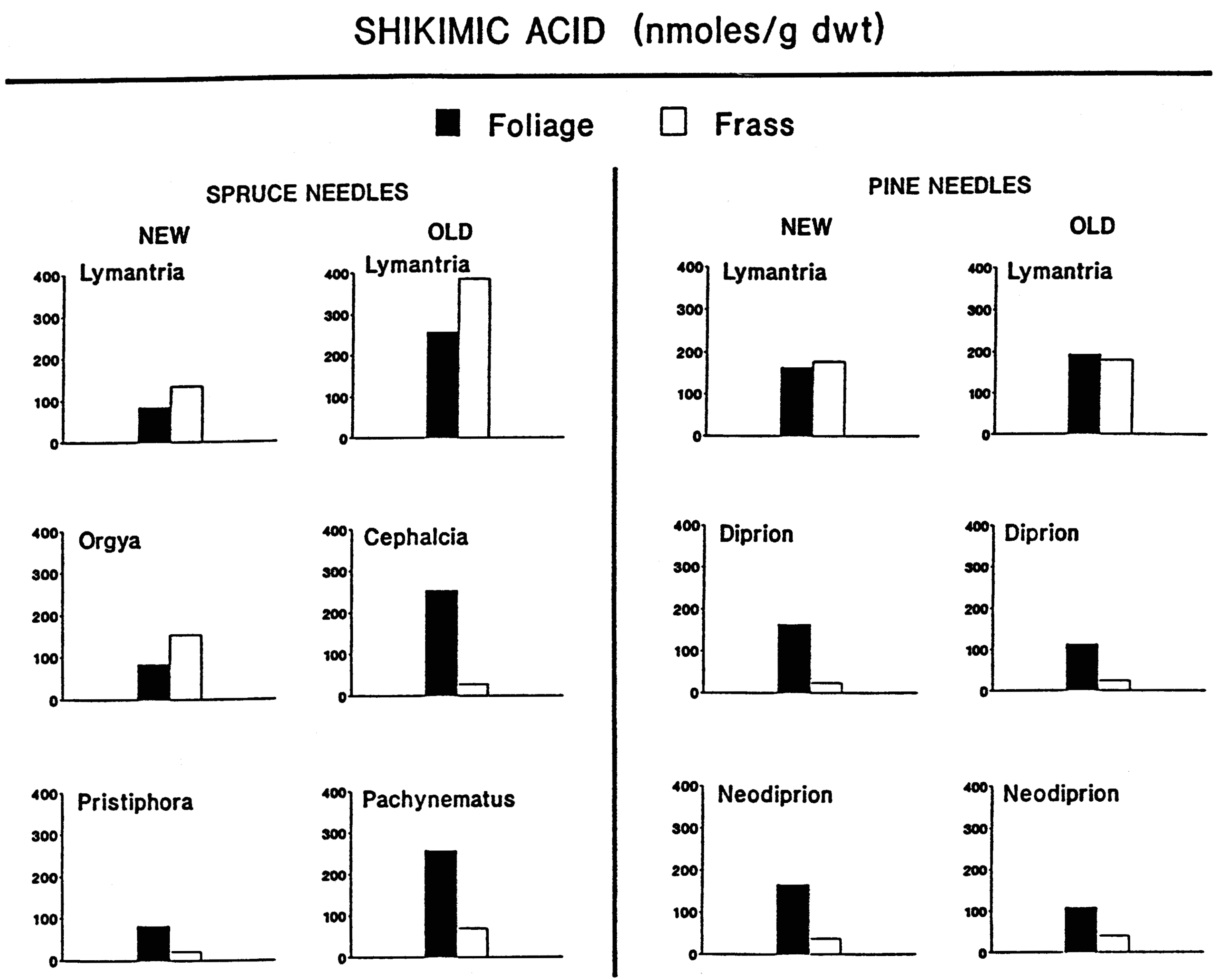

Figure 5. Concentrations of shikimic acid in conifer needles and in herbivore frass.

Likewise the variability of shikimic acid utilization by needle-feeding insects is considerable. The concentration of shikimic acid in the feces of *L. monacha* is often higher than in the food, indicating that the compound passes through the intestine unmetabolized. The same holds for another generalist lepidopteran, *Orgya antiqua*, and the pine specialist lepidopterans, *Bupalus pinarius*, *Dendrolimus pinus*, and *Panolis flammea*.

In contrast, all specialist sawflies, irrespective of host plant and plant part, show fairly high utilization of shikimic acid.

DISCUSSION

The results of our analyses clearly show that in all conifer insect species investigated, the utilization of carbohydrates (fructose, glucose, and sucrose) was almost 100 percent. This strongly suggests that demand for carbohydrates in the concentrations found in conifer needles is high among needle-feeding herbivores. It also suggests that carbohydrates may be a limiting factor in certain performance parameters for those insect species consuming the most carbohydrate-poor diet.

Studies of insect performance in relation to carbohydrate concentrations have so far given rather different results, however. Positive correlations have been found in *Gilpinia hercyniae/Picea abies* (Schopf 1986, Jensen 1988), *Sphinx pinastri/Pinus silvestris* (Otto 1970), and *Choristoneura fumiferana/Picea glauca* (Harvey 1974, McLaughlin 1986). Nonsignificant correlations have been described in *C. fumiferana/Abies balsamea* (Shaw et al. 1978).

Although cyclites are carbohydrates, they seem to differ from them in having a somewhat lower utilization rate. In particular, pinitol, when highly concentrated in the needles, is sometimes found in high concentrations in the feces as well. In any case, the cyclites add to the general pool of energy available to the herbivores.

Nitrogen is one of the compounds most often related to insect performance (Mattson 1980, Mattson and Scriber 1987). Thus it is interesting to note that in the present investigation nitrogen was found to be utilized only to a limited degree by the foliage-feeding herbivores. This may be due to the indigestible nature of the N compounds or to large concentrations of digestibility-reducing compounds, e.g. tannins or resins, which can lower the bioavailability of the proteins in the needles (Rhoades 1983). As nitrogen utilization was low and the concentration of nitrogen high in the feces of species eating newly flushed needles, however, concentrations of digestibility-reducing compounds should also be high in these new needles. This is not consistent with general theory and not supported by available data. By way of explanation, one could argue that the results obtained here are derived mainly from later instar larvae and that newly hatched larvae would have a greater demand for and therefore a higher utilization of nitrogen.

The highly variable utilization of quinic acid and shikimic acid may be interpreted in relation to their potential role as secondary compounds. Utilization of these acids is rather low among generalist and specialist lepidopterans, and the part of the compounds excreted. Accordingly, these insect species do not receive the potential carbon-energy from the compounds in question, but have, on the other hand, developed a tolerance for acidity and merely excrete the acids.

The specialist sawflies, unlike the lepidopterans, seem to metabolize part of the acids and hence obtain carbon-energy, probably by means of microbial activity in the mid-gut (Schopf 1986), but this adaptation often limits them to a very specific host-range, some of the species being unable to tolerate needles of a certain age class even from their favorite host. *Gilpinia hercyniae* often dies on immature spruce needles (Jensen 1988). *Neodiprion sertifer* and *Diprion pini* have a high preference for old, pine needles, though if forced to eat new needles, they are able to survive.

CONCLUSIONS

Results of the present investigation seem to indicate that the main differences in utilization of nutrients and secondary compounds within the needle-feeding guild exist along taxonomical lines (Hymenoptera-Lepidoptera) rather than generalist-specialist lines. Both orders have developed a high capacity of carbohydrate utilization and perhaps a lower capacity of nitrogen utilization. Both specialist and generalist lepidopterans seem unable to metabolize, but able to tolerate certain secondary compounds, whereas hymenopterans, all specialists, utilize these compounds to varying degrees.

SUMMARY

The nutrient content and the content of certain low molecular secondary compounds of conifer needles and flowers from *Picea* and *Pinus* species were quantified by means of gas chromatography and micro-Kjeldahl analysis. The same compounds were also quantified in the feces of conifer insects (Lepidoptera and Hymenoptera) within the herbivore guild. Carbohydrates and cyclites in the needles and in the flowers were almost totally utilized by these insect species, whereas only 45 to 55 percent of the total nitrogen content was utilized. Among specialist and generalist lepidopterans, secondary compounds such as shikimic acid and quinic acid were utilized only to a very low degree, whereas among specialist hymenopterans (sawfly species), utilization of these compounds was high.

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