Seasonal and age-related variation in the needle quality of five conifer species

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Summary. Age changes of foliage resource quality (water, nitrogen, fibre, phenolics and toughness) were studied in five species of conifer (*Pinus sylvestris* L., *Picea abies* (L.) Karsten, *Tsuga heterophylla* (Rafinesque) Sargent (all Pinaceae), *Chamaecyparis lawsoniana* (Murray) Parlato and *Thuja plicata* D. Don (both Cupressaceae) over a 2-year period in an English forest. Mature foliage of *Pinus sylvestris* was characterized by higher levels of nitrogen, fibre and toughness, and lower phenolics, and that of *Tsuga heterophylla* by higher levels of phenolics, and lower fibre and toughness levels, than the mature needles of the other species studied. Immature needles had higher levels of water and nitrogen, and lower levels of fibre and toughness, than older needles. Immature needles of *Picea abies* and *Tsuga heterophylla* had a high concentration of phenolics, which decreased with needle maturity. By mid-August, the levels of most of the foliar constituents in current-year needles had stabilized at levels maintained for the next year. Sampling revealed a fall in the concentration of phenolics, fibre and water in mature needles between March and June. Possible reasons for this seasonal trend are discussed. The levels of conifer foliar constituents were compared with levels recorded in broadleaf trees. Conifers had greater concentrations of all measured foliar constituents, but, with the exception of the six fold greater toughness of conifer needles, the differences between broadleaves and conifers were less than those between the immature and mature conifer needles. Previous studies have related the abundance of Lepidoptera on conifers to hostplant taxonomic relationships. However, the foliar constituents measured in this study were poor predictors of taxonomic relationships between the conifers. It is suggested that the abundance of Lepidoptera on conifers is not determined by levels of general foliar constituents and the role of other hostplant factors in shaping lepidopteran utilization of conifers is discussed.

Key words: Seasonal variation – Nutritive quality – Conifers – Herbivory – Taxonomic relationships

Chemical and physical characteristics of leaves have been measured as indicators of leaf resource quality. Some of these are fundamental chemical and physical attributes of the food, e.g. water, nitrogen, fibre, phenolics and toughness, and represent major defensive costs to the plant (Coley 1983). These foliage characteristics can affect the preference, activity, survival rate and reproductive success of phytophagous insects.

Scriber (1977) and Reese and Beck (1978) have described leaf water as a limiting resource for a variety of phytophagous insects. The low water level naturally found in some tree leaves may restrict the growth rate of larvae (Scriber and Slansky 1981). Likewise, leaf nitrogen levels may limit the development of phytophagous insects (McNeill and Southwood 1978; Mattson 1980) and leaf nitrogen levels have been linked with susceptibility of trees to attack by defoliating insects (Haukioja et al. 1985; White 1984). Water and nitrogen concentrations may act synergistically rather than additively (Scriber and Slansky 1981), with Mattson and Scriber (1987) suggesting that foliage water and nitrogen levels may be key variables describing the feeding success of phytophagous insect larvae.

The digestibility of foliage may be physically reduced by high concentrations of fibre (consisting of cellulose, hemicellulose and lignin), and leaf toughness, and may also be chemically reduced by plant secondary chemicals, e.g. phenolics (Mattson and Scriber 1987).

Fibre is recognised as an important factor in vertebrate forage consumption (Mattson and Scriber 1987) but its role in invertebrate nutrition has been little researched. However, fibre concentration in conifer needles has been implicated in reducing digestibility and larval survival in some phytophagous insects (Fogal 1974; Omlin and Herren 1976).
Leaf toughness increases rapidly as a new flush of leaves matures, and this is thought to inhibit feeding in some spring-feeding Lepidoptera (Feeny 1970; Hough and Pimentel 1978) and correlates negatively with leaf damage caused by insect herbivory (Coley 1983). Toughness may be important in increasing mortality of newly hatched larvae (Tanton 1962), and it was the leaf characteristic that best explained the difference in the performance of Paropsis atomaria Oliver (Coleoptera: Chrysomelidae) on mature and immature eucalyptus leaves (Larsson and Ohmart 1988).

Plant secondary chemicals are assumed to have an important role in insect-plant interactions (Feeny 1976; Rhoades and Cates 1976; but see Bernays 1981). Certain specific secondary chemicals have been implicated as feeding deterrents in conifers (Ikeda et al. 1977; Jensen 1988).

Most studies of conifers have involved sampling the trees as if they were deciduous, i.e. sampling from May to September. However, larvae can be found feeding on conifers throughout the year (Hatcher 1989) and there is evidence that late-year (October–December) (Tamm 1955; Woodwell 1974), and spring changes in the foliar constituents in mature needles (Oren and Schulze 1989) also occur. Studies on conifers have mainly concentrated on the mineral nutrition of the trees, and some needle characteristics of potential importance to phytophagous insects, e.g. needle toughness and fibre concentration, have been little studied.

Hostplant use by conifer-feeding Lepidoptera is heavily determined by conifer taxonomic relationships (Hatcher 1990; Holloway and Herbert 1979) with conifers in the family Cupressaceae having a depauperate Lepidoptera fauna (Alfaro et al. 1981; Hatcher 1990) (Table 1). This study aimed to determine whether such taxonomic relationships were manifested in conifer foliage quality.

A previous study investigated the conifer-feeding macro-Lepidoptera fauna of an English woodland (Hatcher 1990) (Table 1). In this study I examine the seasonal patterns and age-related changes in foliage chemistry of the five species of conifer: *Pinus sylvestris* L., *Picea abies* (L.) Karsten, *Tsuga heterophylla* (Rafin.-esque) Sargent (all Pinaceae) and *Chamaecyparis lawsoniana* (Murray) Parlatore and *Thuja plicata* D. Don (both Cupressaceae), for which the Lepidoptera fauna and their ability to feed on these conifers is known (Table 1). Five parameters of foliage resource quality (water, nitrogen, phenolics, fibre and toughness) were chosen on the basis of their importance in determining feeding success in phytophagous insects, and both the current and previous year’s age-class of needle were examined.

Several species of polyphagous, normally broadleaf-feeding, Lepidoptera have been recorded feeding on conifers (Hatcher and Winter 1990). The foliage resource quality of the five species of conifers is compared with that of broadleaf trees to suggest possible nutritional problems these larvae have had to overcome in their switch from feeding on broadleaf trees to conifers.

### Materials and methods

#### Study area

The study was carried out in Bernwood Forest, 10 km north-east of Oxford, England (NGR SP 6010).

Conifers have been planted in this deciduous forest since at least 1850 (Thomas 1987). During the 1950s and 1960s Bernwood Forest was replanted with a variety of conifer species in pure plantings and also mixed with broadleaf trees. At present Bernwood Forest is predominantly planted with *Picea abies*. Four other species of conifer have also been planted in Bernwood Forest over an area greater than 2 ha: *Pinus sylvestris*, *Tsuga heterophylla*, *Chamaecyparis lawsoniana* and *Thuja plicata*. These five species were sampled in this study.

A sample stand consisting of a pure planting of each of the species of conifer was selected. These stands were of a similar age (22–31 years old at end of study) and height (5–8 m at end of study). All the stands were on Oxford clay, except the *Pinus sylvestris* stand which was on alluvium.

#### Sample collection and phytochemical analysis

Needles produced in 1986 (1986 age-class) were sampled throughout 1987. The new needles produced in 1987 (1987 age-class) were sampled from the time of bud-burst in late April 1987 until the end of 1988, and the new needles produced in 1988 (1988 age-class) were sampled from April until December 1988. This enabled two comparisons between different age-class needles to be carried out, and the effect of needle ageing on foliage resource quality to be studied on a set of needles for 20 months.

Foliage samples were taken at 21-day intervals. On each occasion five trees on the edge of each of the sample stands were selected at random. One branch was removed from each tree at about 1.75 m height between 1000 and 1200 hours BST.

Although needles from branches below the tops of trees can have a different nutrient concentration from those in the tops of trees (Jensen 1988; Tyrrell and Boerner 1987; White 1954), studies on the nutrition of Lepidoptera larvae feeding on the conifers in Bernwood Forest have utilized foliage and larvae collected from this height (Hatcher 1989) and thus comparisons are valid. Also, edge trees were the only ones to have foliage at a height that could be readily sampled.

Each branch sample was placed in a paper bag and processed within 2 h of removal. Needles, or scale leaves, were cut from branches and separated into age-classes. Although this was straightforward for members of the Pinaceae, the twigs of the two

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**Table 1.** Macro-Lepidoptera recorded on conifers in Bernwood Forest 1986–1988. Data from Hatcher (1989). Abbreviations after species names refer to conifers in Bernwood Forest the moths were recorded from, and could complete larval development on: Ps = *Pinus sylvestris*, Pa = *Picea abies*, Th = *Tsuga heterophylla*, Cl = *Chamaecyparis lawsoniana*, Tp = *Thuja plicata*

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<td><em>Odontopera hildenata</em> (Clerck) (Geometridae):</td>
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<td><em>Deileptenia ribeata</em> (Clerck) (Geometridae):</td>
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<td><em>Alcis repandata</em> L. (Geometridae):</td>
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<td><em>Hylaea fasciaria</em> (L.) (Geometridae):</td>
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<td><em>Panolis flammea</em> (D. &amp; S.) (Noctuidae):</td>
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