This is to certify that the

dissertation entitled

PHENOLOGICAL VARIATION IN THE SUSCEPTIBILITY OF WHITE SPRUCE TO THE SPRUCE BUDWORM

presented by

ROBERT KENT LAWRENCE

has been accepted towards fulfillment
of the requirements for

PH.D. degree in ENTOMOLOGY

William Mattson
Major professor

Date July 9, 1990

PHENOLOGICAL VARIATION IN THE SUSCEPTIBILITY OF WHITE SPRUCE TO THE SPRUCE BUDWORM

By

Robert Kent Lawrence

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology
and
Program in Ecology and Evolutionary Biology

1990

ABSTRACT

PHENOLOGICAL VARIATION IN THE SUSCEPTIBILITY OF WHITE SPRUCE TO THE SPRUCE BUDWORM

By

Robert Kent Lawrence

Seasonal and maturational changes in plant traits create temporal windows of susceptibility during which the plant is a suitable host for various herbivores. Synchrony of insect phenology and host tree phenology has often been suggested as a factor in the susceptibility of white spruce, *Picea glauca* (Moench) Voss, and other host species to the spruce budworm, *Choristoneura fumiferana* (Clemens). Although the concept of phenological windows of susceptibility has long existed, this study is the first to test the hypothesis comprehensively and to substantiate it. Phenological variation in white spruce susceptibility was evaluated by measuring performance of several cohorts of spruce budworms caged on trees at different phenological stages of the hosts and comparing budworm performance with phenological variation of 13 foliar traits.

The window of susceptibility in white spruce was well defined in this study. Performance is high for budworms that emerge and begin feeding during the 3-4 weeks prior to budbreak and complete larval development prior to the end of shoot growth. Larval survival averaged greater than 60% for budworms that began development 1-3 weeks prior to budbreak, but decreased to less than 10% for budworms that began development two or more weeks after budbreak. More

than 85% of total larval mortality occurred by the time most larvae were third instars in both early and late budworm cohorts.

Variation in budworm larval survival and length of development (degree days) among three white spruce seed sources was clearly linked to phenological differences among seed sources. Variation in budworm weight, growth rate and length of development (days) among seed sources was positively correlated with tree growth rate, thereby implying that competition for resources within individual trees may affect their susceptibility to insects.

Levels of nitrogen, phosphorous, potassium, total sugars and water in current-year foliage declined, while leaf toughness increased, during spring and early summer. Calcium, magnesium, copper and zinc declined and later increased. High water content and low leaf toughness are strongly correlated with high budworm performance and are the foliar traits most likely to be key factors defining the window of susceptibility in white spruce.

To Martha, who lovingly made many sacrifices and
contributed to my success in countless ways during a time
when she was laboring on her own doctoral program,
and
To my parents, who first introduced me
to the fascination of the biological sciences
and who have always given their love and support.

ACKNOWLEDGMENTS

I would like to express my sincere thanks to Dr. William J. Mattson, my major professor, for his guidance and his friendship. I learned a great deal from him about how to think as well as to do. His unselfish support and encouragement throughout my lengthy research program has been greatly appreciated. He and his wife, Sheri, have been true friends. Choosing to work with Bill was one of my better decisions.

I would also like to thank the members of my graduate committee for their many contributions. Dr. James W. Hanover was exceptionally generous in allowing me to conduct experiments in his forest genetics plantations and in providing laboratory facilities for a special research project. I enjoyed taking his classes and have appreciated his advice and friendly cooperation. Dr. John A. Witter provided valuable guidance and played a key role as motivator. I appreciated his occasional friendly suggestions concerning my research velocity. I am very grateful to Dr. Gary A. Simmons for his advice, encouragement and willingness to listen to concerns both personal and professional. I enjoyed the opportunity to assist Gary in teaching, and hope that I can be as enthusiastic and effective as he in my own future teaching endeavors. My thanks go to Dr. James R. Miller for providing constructive criticism from the vantage point of one who is not so close to the trees.

Special thanks are extended to the North Central Forest Experiment Station of the U. S. D. A. Forest Service for sponsoring my research program. The continued financial support throughout my program was deeply appreciated.

I am indebted to my co-workers for their assistance, their patience and their friendship. Dr. Robert A. Haack gave valuable assistance in many areas. He made important contributions to this research with his observations, discussions and suggestions during the early phases of my work. He shared many long days in the field and lab assisting in my experiments as well as maintaining his own. My sincere thanks goes to Bruce A. Birr for his persistence and patience in doing all of the foliar nitrogen and mineral analyses. He made my work much easier by providing valuable support in many ways in both the field and lab. I also thank fellow graduate student, Daniel A. Herms, for many stimulating conversations and helpful suggestions. Thanks also go to Richard Blank for doing foliar sugar analyses and to Kwei-Fong Hao, Brian Mitchell and Brian McLaughlin for successfully accomplishing many tedious tasks of sample preparation and data collection.

I appreciate the advice given by Dr. Carl W. Ramm on techniques of multivariate statistical analysis. I also thank Tom Stadt and John Vigneron of the W. K. Kellogg Experimental Forest for providing valuable support to my field research and Bill Dunn of the Huron-Manistee National Forest for providing temperature data.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

WINDOWS OF SUSCEPTIBILITY

Plant resistance against herbivory involves a combination of many host-plant traits including nutrients, allelochemics, physical attributes and bio-associations. However, plant traits are not invariant. They typically vary spatially and temporally, as does the suitability of a host to herbivores (Mattson et al. 1982). Spatial variation occurs within and among individual plants and among populations (Whitham 1981, 1983, Krischik and Denno 1983). Temporal variation can exist as diurnal, seasonal or ontogenetic changes in plant traits and as changes induced by biotic or abiotic agents (Mattson et al. 1982, Raupp and Denno 1983).

For each herbivore, there is a range of values for each host-plant trait that is suitable for growth and survival of the herbivore. Plants may pass through a temporal suitability/susceptibility "window" when plant trait values optimally match with herbivores' tolerance ranges for plant traits (Feeny 1976, Lawton and McNeill 1979, Mattson et al. 1982, Mooney et al. 1983). Such windows of susceptibility are associated with both phenological and ontogenetic changes in host quality. The success of an herbivore on a given host plant therefore depends on the degree of its synchrony with host phenology.

Phenological Variation in Plant Traits

Many plant traits that affect the suitability of a host plant to herbivores vary seasonally or, in other words, with leaf age (Raupp and Denno 1983, Cates

1987, Mattson and Scriber 1987). Among these traits are the foliar levels of water (Hinckley et al. 1978, Scriber and Slansky 1981), nitrogen (McNeill and Southwood 1978, Mattson 1980), mineral elements (Mattson and Scriber 1987, Clancy et al. 1988a), fatty acids (Clark et al. 1975), carbohydrates (Little 1970, Chapin et al. 1986), phenolics (Feeny 1970, Rossiter et al. 1988), terpenoids (von Rudloff 1972, Cates and Redak 1988), alkaloids (McKey 1974), epicuticular waxes (Hanover and Reicosky 1971) and physical attributes such as leaf toughness and fiber content (Feeny 1970, Coley 1983, Mattson and Scriber 1987).

The levels of water and nitrogen in leaves are positively correlated and both decline strongly with leaf age (Scriber and Slansky 1981, Scriber 1984b, Mattson and Scriber 1987). These patterns consistently occur in most plant growth forms (e.g. grasses, forbs, trees). However, levels of both water and nitrogen are usually lower in trees than in herbaceous plants, and lower in evergreen trees than in deciduous trees. The levels of water and nitrogen in very young leaves of trees approach those found in herbaceous plants (Mattson and Scriber 1987). Insect herbivore performance (e.g. growth rates and food utilization efficiencies) is usually positively correlated with foliar levels of both water and nitrogen (Scriber and Slansky 1981, Scriber 1984b, Mattson and Scriber 1987). Although water and nitrogen are not the only factors affecting insect performance, they effectively reflect the milieu of plant traits encountered by the herbivore (Scriber 1984b, Mattson and Scriber 1987), and together these two plant traits provide an index of plant quality, which can be used to predict maximum growth performance of insect herbivores (Scriber 1984b).

Plant nitrogen varies qualitatively, as well as quantitatively, with advancing plant phenology (McNeill and Southwood 1978, Mattson 1980). Nitrogen content of young plant tissues consists primarily of amino acids, soluble

proteins and nitrogen-based secondary compounds, while the nitrogen content of older tissues consists primarily of structural or insoluble protein (Mattson 1980).

Seasonal variation of foliar mineral concentrations is relatively consistent for several mineral elements among many woody plant species. For example, phosphorous and potassium levels decrease rapidly during the growing season, whereas calcium, manganese and aluminum may increase almost linearly (Grigal et al. 1976, Mattson and Scriber 1987, Clancy et al. 1988a, Hockman et al. 1989). The seasonal trend for magnesium is less consistent, with foliar concentrations increasing, decreasing, or sometimes first decreasing and then increasing later in the season (Grigal et al. 1976, Mattson and Scriber 1987, Clancy et al. 1988a). Micronutrients such as boron, copper, iron, zinc and sodium may also rapidly decrease early in the growing season and later increase (Mattson and Scriber 1987).

Seasonal variations in concentrations of carbohydrates in temperate woody plants reflect the dynamics of photosynthesis, carbon metabolism and translocation of assimilates (Loach and Little 1973, Bernard-Dagan 1988). Energy reserves (e.g. starch, sugars, lipids) are metabolized before the start of growth and translocated from storage sites in roots, stems and shoots to new leaves and other growing points (Kramer and Kozlowski 1979, Bernard-Dagan 1988). As photosynthesis increases and new leaves become net producers of carbohydrates, assimilates are exported from leaves to other parts of the plant. Seasonal patterns of non-structural carbohydrates differ among plant growth forms (Kramer and Kozlowski 1979, Chapin et al. 1986). Annual fluctuations in concentrations of non-structural carbohydrates are much less in evergreen plants than in deciduous plants. In evergreen plants a large portion of reserve carbohydrates are stored during the winter in old leaves, and then translocated to new leaves during initial growth stages in the spring (Ericsson 1978).

Foliar levels of allelochemics can vary considerably with plant phenology. Levels of phenolic compounds typically increase throughout the growing season (Feeny 1970, Haukioja et al. 1978, Mattson and Palmer 1988). On the other hand, they may peak at, or within a few weeks after, budbreak and then decline with leaf age (Coley 1983, Baldwin et al. 1987, Mattson et al. 1988, Rossiter et al. 1988). The total quantity of terpenes in current-year conifer foliage increases during the growing season (von Rudloff 1972, Cates and Redak 1988). However, the greatest changes in relative amounts of terpenes in conifer foliage often occur in buds prior to budbreak or in new leaves just after maturing during the shoot growth period (von Rudloff 1972, 1975a, 1975b, von Rudloff and Granat 1982). Levels of alkaloids, cyanogenic glycosides and many other toxins are higher in younger leaves than older leaves (McKey 1974, Mattson 1980).

Leaf toughness, a largely unappreciated defense, is directly correlated with leaf maturity (Feeny 1970, Coley 1983, Lowman and Box 1983). Levels of structural components (e.g. cellulose, hemicellulose, lignin) that contribute to leaf toughness increase in maturing leaves (Chung and Barnes 1980, Scriber and Slansky 1981, Mattson and Scriber 1987).

SPRUCE BUDWORM AND HOST PHENOLOGY

Interspecific and intraspecific variation in host tree phenology have often been cited as major factors in the relative susceptibility of host trees to the spruce budworm (*Choristoneura fumiferana* (Clemens)) and western spruce budworm (*C. occidentalis* Freeman) in North America (Blais 1957, Greenbank 1963, Eidt and Cameron 1971, Redak and Cates 1984, Volney 1985, Osawa et al. 1986, Blum 1988) and to the European fir budworm (*C. murinana* Hübner) in Europe (Schönherr 1980). Annual variations in host tree susceptibility have been, in some cases, attributed to climatic effects that alter the synchrony of budworm phenology and host tree phenology (Schönherr 1980, Beckwith and Burnell 1982, Thomson et al. 1984, Shepard 1985).

The spruce budworm is a micro-lepidopteran folivore of boreal North America. Its primary hosts are balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss), but the budworm can cause significant damage to red spruce (*P. rubens* Sarg.), black spruce (*P. mariana* (Mill.) B.S.P.) and subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) (Harvey 1985). Periodic outbreaks of this insect have resulted in many millions of hectares of defoliated and killed trees in northeastern North America (MacLean 1985, Hardy et al. 1986).

Emergence and development of spruce budworm larvae in the spring generally coincides with budbreak and shoot elongation of its host trees (McGugan 1954, Greenbank 1963). The larvae overwinter on trees as 2nd instars and emerge from their hibernacula shortly before budbreak. Larvae initially mine

either old needles, staminate flowers if present, or unopened vegetative buds. Most larvae mine one-year-old needles prior to vegetative budbreak (McGugan 1954, Blais 1979). When vegetative buds begin to swell and flush, budworm larvae move to this new foliage where they generally remain until they complete development. However, at high population densities some "backfeeding" on old foliage occurs.

Observations from several field and laboratory studies indicate that asynchrony of budworm phenology and host tree phenology results in reduced performance (poorer survival, growth and fecundity) of the insect (Greenbank 1956, Eidt and Little 1970, Eidt and Cameron 1971, Mattson et al. 1983, Thomas 1983, Blake and Wagner 1986, Thomas 1987). Negative effects of asynchrony on budworm performance have been observed both when insect phenology is advanced and when it is retarded in relation to tree phenology.

When budworm phenology is advanced in relation to tree phenology (larval emergence precedes budbreak by several days), the young larvae are not able to penetrate the tight vegetative buds and must then feed on mature foliage for an extended period. Larval mortality increases under these conditions (Blais 1957, Eidt and Cameron 1971, Shepard 1985) and is presumably caused by either deleterious effects of a less suitable diet or by losses due to increased dispersal of larvae as they search for acceptable feeding sites.

When budworm phenology is retarded in relation to tree phenology (larval emergence follows budbreak by several days), reduced performance by the budworm is reflected by several measures (lower survival, lower body weight, longer development time, lower relative growth rate, lower efficiency of conversion of ingested food and lower fecundity) (Greenbank 1956, Mattson et al. 1983, Blake and Wagner 1986, Thomas 1987). Older foliage appears to be less

suitable food for budworms, but the precise mechanisms of these effects are not known.

These patterns of insect performance indicate that a phenological window of susceptibility to the spruce budworm exists in its host trees. The timing or phenological limits of this window have not been determined, nor have the causes of reduced budworm performance been clearly identified. A variety of test conditions were used in previous studies of spruce budworm phenological synchrony. In some cases only late-instar larvae and/or only one or two levels of asynchrony were used. Excised foliage or potted seedlings were used in laboratory studies. In some cases, analyses of the phenological variation in plant traits were minimal or non-existent. No study has examined the question comprehensively using complete larval development, several levels of asynchrony, non-juvenile trees under field conditions, and measurements of seasonal variation in several plant traits.

WHITE SPRUCE BIOLOGY

White spruce, *P. glauca*, has a transcontinental distribution which extends from Alaska to Newfoundland and northward to the treeline in northern Canada. Its range extends southward into the United States from Minnesota to Maine with isolated populations in Montana, South Dakota and Wyoming (Fowells 1965). Western portions of the range of white spruce overlap with the ranges of Engelmann spruce (*P. engelmannii* Parry) and Sitka spruce (*P. sitchensis* (Bong.) Carr.). White spruce hybridizes with these two species in broad zones of introgression (Roche 1969, Nienstaedt and Teich 1972).

Genetic variation among white spruce populations has been studied for many morphological and physiological traits (Wilkinson et al. 1971, Nienstaedt and Teich 1972, Canavera and DiGennaro 1979, Nienstaedt 1985, Khalil 1985, 1986). The results of several studies suggest that white spruce consists of two or three east-west clines (Wilkinson et al. 1971, Nienstaedt and Teich 1972, Khalil 1985). Seed sources in the Ottawa Valley along the Ontario-Quebec border have consistently produced the fastest growing white spruce (Nienstaedt 1969, Wilkinson 1977b, Wright et al. 1977, Genys and Nienstaedt 1979, Khalil 1985).

Vegetative growth phenology of white spruce, specifically the timing of bud flushing, is under strong genetic control (Nienstaedt and King 1970, Wilkinson 1977a, Nienstaedt 1985). The variation in timing of bud flushing among individuals in white spruce provenance and progeny tests has ranged from a span of 12 days to a span of 35 days (Wilkinson 1977a, Blum 1988).

OBJECTIVES

The objectives of this study were to: 1) test the hypothesis that a phenological window of susceptibility to spruce budworm exists in white spruce, 2) determine the exact timing and duration of such a window of susceptibility, 3) describe phenological changes in key host nutritional factors that are related to host susceptibility, 4) determine how these changes in plant traits are related to the performance of the spruce budworm and 5) evaluate the effect of early and late-flushing seed sources on host susceptibility. In addition, there were other more specific questions addressed in relation to the above objectives. I hypothesized that (a) early and late-flushing seed sources will differ only in their shift in timing of phenological events, (b) insect-host asynchrony affects the budworm survivorship curve primarily by causing a rise in early larval mortality and (c) phenological changes in plant nutritional factors have different effects on younger larvae and older larvae.

MATERIALS AND METHODS

A major experiment was conducted in 1985 to test the phenological window of host susceptibility hypothesis for the spruce budworm and to determine the effects of insect-host asynchrony on several measures of budworm performance. A similar experiment in 1987 examined the effects of insect-host asynchrony on the budworm survivorship curve. Seasonal variation in foliar traits were measured in 1985 and 1986, which allowed comparison with insect performance data from 1985 to evaluate the relationship between host susceptibility and host phenology.

Experiments were conducted in a white spruce provenance plantation located in Wexford Co., Michigan in the Huron-Manistee National Forest. The trees were 27 years old in 1985, and were part of the White Spruce Seed Source Variation Study G-113, which was established by the USDA Lake States Forest Experiment Station (North Central Forest Experiment Station) in 1962.

Phenological Window of Susceptibility

Phenological variation in host susceptibility was evaluated by measuring spruce budworm performance at varying levels of synchrony between budworm and host tree phenology. Synchrony was manipulated by using host trees from three seed sources that differed in their timing of bud flushing and by introducing eight cohorts of spruce budworm to the trees at different phenological stages of the hosts.

A factorial experiment was used where the main effects were white spruce seed sources and spruce budworm cohorts. Information on the relative timing of budbreak among seed sources was obtained from the Dept. of Forestry, Michigan State University (unpublished data). Seed sources 1665 from Stony Rapids, Saskatchewan (SASK) and 1677 from Fort McLeod, British Columbia (BC) were selected as the early and late-flushing seed sources, respectively. Seed source 1663 from Beachburg, Ontario (ONT) is an intermediate to late-flushing seed source that also was selected because of its unusually good growth characteristics. It has consistently been one of the fastest growing seed sources among several plantations in the northeastern U.S. and Canada (Nienstaedt 1969, Wilkinson 1977b, Wright et al. 1977, Genys and Nienstaedt 1979). Eight trees were randomly selected as study trees from among the more open-grown trees in each seed source.

Spruce Budworm Cohorts

Spruce budworm larvae used in this experiment were obtained from a colony maintained by the Insect Rearing Service of the Forest Pest Management Institute, Forestry Canada in Sault Ste. Marie, Ontario. Larvae were received from the stock colony as overwintering 2nd instars enclosed in their hibernacula on gauze strips. Larvae were stored at ca. 5 °C until used in the field. Eight cohorts of 2nd-stage larvae were caged on the trees during the spring and summer of 1985. Each cohort began at a different time in the host tree's phenology. A gauze patch containing approximately 30 larvae was enclosed in a small-mesh nylon sleeve cage (70 cm length) on one mid-crown branch on each tree for each cohort. Therefore, 24 branches (3 seed sources x 8 trees/seed source) were caged for each cohort. Cages were located on all sides of each tree to prevent excessive destruction of foliage on one side when branches were later removed from the

tree. Cage positions were uniformly distributed around the tree circumference within each seed source and budworm cohort.

I started the first cohort of budworm larvae at approximately the same time as spring emergence of natural, field populations of budworm 2nd-instars. After reviewing the literature (Henson 1948, Bean 1961, Cameron et al. 1968, Miller et al. 1971, Shaw and Little 1973, Thomas 1976), I estimated peak emergence in the field to occur at 50 to 100 degree days based on a threshold of 5.6 °C and a start date of 1 March. The first budworm cohort was placed on the trees on 23 April at ca. 173 accumulated degree days (about four calendar days after the estimated peak of emergence of natural budworm populations). The next five cohorts were started at weekly intervals through 28 May (Table 1). The seventh and eighth cohorts were started four and eight weeks later on 25 June and 23 July, respectively.

Each cohort remained on the trees for six to seven weeks until most of the budworms were in the pupal stage. At that time all caged branches of that cohort were cut from the trees and examined in the laboratory. The first cohort was removed from the trees on 5 June, and the last cohort was removed on 10 September. All budworms were collected from the caged branches and held in individual plastic vials at ca. 23 °C until adult emergence. Adults were killed by freezing within 24 hours after emergence, and then dried in an oven at 60 °C for 48 hours prior to being sexed and weighed. Budworms that were still in the final larval stage when collected from the cut branches were provided with current-year foliage from the seed source on which they had been caged, and allowed to complete development in petri dishes. Larvae that did not pupate within four days after the cohort was removed from the trees, were not included in analyses of body weight.

Table 1. Dates and accumulated degree days when each spruce budworm cohort was placed on white spruce trees in 1985.

Cohort	Julian Date	Gregorian Date	Accumulated Degree Days[1]
1	113	23 April	173
2	120	30 April	234
3	127	7 May	296
4	134	14 May	406
5	141	21 May	471
6	148	28 May	556
7	176	25 June	900
8	204	23 July	1373

[1] Base = 5.6 °C; Start date = 1 March

To provide fresh, vigorous insects for all cohorts, larvae were received in three batches from the Canadian stock colony and stored (5 °C) no more than five weeks prior to use in the field. Cohorts 1 to 3 were taken from the first batch (April), cohorts 4 to 6 from the second batch (May), and cohorts 7 and 8 from the third batch (June).

The variability of budworm vigor among batches was evaluated by examining the performance of budworms reared on artificial diet (McMorran 1965) as part of other feeding studies in 1985. These insects came from batches received from the stock colony in January, March, June and November. They were used in control treatments in laboratory feeding studies and maintained at 22 °C and a photoperiod of 16:8 hr (light:dark).

Tree Phenology

The phenological stage of buds and percent shoot elongation on study trees were monitored at weekly intervals until growth ceased. Bud phenological stage was rated and shoot elongation was measured on two randomly selected terminal shoots on both the north side and south side at mid-crown level of each tree. The phenological stage of the terminal bud on each shoot was rated using a 6-point system following Nienstaedt and King (1970):

Phenological Stage	Rating
Bud in winter condition	1
Bud beginning to swell	2
Bud globose; swelling prominently	3
Bud green; bud scales expanding and thinning but still intact	4
Bud scales separating and exposing green needles	5
Shoot elongating	6

The first measurement of shoot elongation was made in April prior to noticeable swelling of most buds and consisted of total bud length. Elongation measurements included bud expansion prior to budbreak and elongation of the shoot after budbreak.

Ambient temperature in the plantation was measured using a recording hygrothermograph. Cumulative degree days (threshold = 5.6 °C) from 1 March were computed using a sine-wave method (Allen 1976).

Spruce Budworm Survivorship Curve

The effect of host phenology on the survivorship curve of the spruce budworm was examined in 1987 in the same white spruce plantation. An "early" cohort and a "late" cohort of budworms were placed on 10 trees of the Beachburg, Ontario seed source (#1663) using techniques similar to those used in the 1985 study. However, in 1987, budworm survival was evaluated at several points during the developmental period of each cohort, rather than only at pupation. Budworms were caged on five mid-crown branches of each tree for each cohort. One caged branch was removed from each tree at four 7 to 8-day intervals during budworm development. The final caged branch on each tree was removed when the majority of budworms were in the pupal stage. Branches were examined in the laboratory under a lighted magnifying lens, and budworm survival was determined for each sample date. The average developmental stage of budworm larvae was determined for each sample date by preserving all collected larvae in 70% ethanol and measuring head capsule widths using an ocular micrometer in a dissecting microscope (McGugan 1954, Bean and Batzer 1957, Crummey and Otvos 1980).

The first cohort in the 1987 experiment was placed on the trees on 10 April at ca. 133 accumulated degree days, slightly earlier than the first budworm cohort in the 1985 experiment. The second cohort was placed on the trees on 1 June at ca. 760 accumulated degree days, slightly later than the sixth cohort in 1985. Both budworm cohorts in 1987 were taken from the same stock colony batch.

Seasonal Variation in Host Nutritional Traits

Several periodic measurements were made of the phenological condition of the host trees during 1985 and 1986. Foliage samples were collected in 1985 at 1-3 week intervals for analyses of sugar, nitrogen and mineral content. The first collection was made on 1 May, immediately prior to budbreak on the earliest-flushing trees (SASK seed source). Samples were collected on that date from both the previous year's growth ("old" foliage) and from expanding vegetative buds. All subsequent samples were collected from current-year foliage only. Each sample of shoots consisted of ca. 5 g (fresh wt.) of bulked foliage from one tree. In most cases each sample of buds consisted of less than 5 g. Samples were sealed in plastic bags, transported to the laboratory in ice-chilled containers, and stored at -10 °C. Foliage samples were next oven-dried at 60 °C for 48 hours. Foliage (exclusive of twigs and bud scales) was then ground to a fine powder in a Wiley mill, and stored in dry conditions at ca. 22 °C until further processing.

Samples were analyzed for soluble sugar content with a high pressure liquid chromatography (HPLC) technique that extracted 5-, 6- and 12-carbon sugars (Haack et al. 1991). Each sample was prepared by placing 200 mg of powdered foliage and 10 ml of 83:17 acetonitrile/water in a centrifuge tube and shaking the tube for 24 hours in darkness. The sample was then centrifuged

briefly and the supernatant passed through a Sep-pak C_{18} cartridge (Waters Assoc.) to remove particulate matter. Samples were stored in glass vials. Analysis was accomplished by injecting 75 ul of sample onto a Waters HPLC system with a Waters carbohydrate analysis column and differential refractometer and using a mobile phase of 83:17 acetonitrile/water and a flow rate of 2 ml/min. A Hewlett Packard integrator performed data integration. Peaks were identified by comparison with retention times of known standards and quantified by comparison with a calibration curve.

Total nitrogen and total phosphorous were determined with standard micro-Kjeldahl techniques. A 0.15 g sample of powdered foliage was digested with 8 ml concentrated sulfuric acid and a catalyst mixture (1.5 g K_2SO_4 and 175 mg HgO) for one hour at 385 °C. Sample volume was then increased to 75 ml with DI (distilled/deionized) water. Sub-samples of 3 ml were stored in sealed plastic vials and then analyzed colorimetrically with a Technicon Auto-analyzer II.

Totals for elemental minerals (K, Ca, Mg, Mn, Cu, Fe, Na, Zn) were obtained with plasma emission spectroscopy. A 0.40 g sample of powdered foliage was digested with 5 ml of concentrated HNO_3 for one hour at 155 °C. Then 2 ml of 70% $HClO_4$ was added and digestion continued for two hours at 220 °C. One ml of 3% LiCl was added to the sample for ionization suppression, sample volume was increased to 15 ml with DI water, and the sample was stored in polypropylene vials. Samples were analyzed on a Beckman Spectrometrics Spectraspan Model III-A Spectrometer.

Accuracy of total nitrogen and phosphorous analyses and elemental minerals analyses was checked using National Bureau of Standards standard reference materials; agreement was within 5% of certified values. Precision was checked by conducting two separate digestions for ca. 2% of samples; average relative deviations were less than 5%.

Measurements of the phenological variation in leaf water content and leaf toughness were made in 1986 on the same trees studied in 1985. Foliage samples were collected at one to two-week intervals during April-May and at three to four-week intervals during June-August. Tree phenological stage (bud stage and shoot elongation) and ambient temperatures in the plantation were measured in 1986 in the same manner as in 1985.

Foliage samples for analysis of water content were collected on each sample date at about the same time of day (1100-1500 hrs). Samples were taken from the previous year's growth prior to budbreak and from current-year foliage after budbreak. Each sample consisted of one shoot collected from the mid-crown level on the south side of each tree. The needles were immediately cut from each shoot, placed in tightly sealed, pre-weighed plastic vials and transported in cool, dark conditions to the laboratory. No samples were collected at times when moisture (dew or precipitation) was visible on the foliage. Fresh weight of the foliage was determined within 12 hours after collection, and dry weight was determined after 48 hours at 60 °C.

Samples for analysis of leaf toughness were collected at the same time of day and at the same general location on the tree as the water content samples. One shoot was collected per tree, placed in a tightly capped vial, and transported in cool, dark conditions to the laboratory. Samples were stored at ca. 5 °C until further processing. Ten needles were selected from each shoot for measurement of toughness. Toughness was determined by measuring the grams of force required to break a needle using the type of device developed by Feeny (1970). This device uses a cylindrical aluminum shaft (2 mm diam.) to puncture the leaf as force is added to the opposite end of the shaft. A Chatillon fruit puncture gauge (rather than a beaker of sand as in Feeny's technique) was used to apply

pressure to the end of the shaft and to measure the force at which the needle broke.

Statistical Methods

Insect Performance Variables

Spruce budworm performance was measured by computing percent larval survival (2nd instar to pupation) and percent pupal survival (pupation to adult emergence) for individual caged branches, and length of development period (days and degree days), adult dry weight (mg) and growth rate (mg/degree day) for individual insects. To meet the assumption of normality, arcsine transformation was performed on larval survival data prior to data analysis.

Neuter values (sex effect standardized) were computed for budworm weight, length of development and growth rate by converting values for individual males to female-equivalent values. For example, the value of an individual male weight was converted to its neuter value by multiplying the male's weight by the ratio of mean female weight to mean male weight. Neuter values were used in all analyses of weight, length of development and growth rate. This procedure eliminated much redundancy in the data analyses and provided more adequate sample sizes in those treatments with low budworm survival. The patterns of budworm performance were similar for males and females across seed sources and cohorts, although females generally had greater body weight and longer development times.

Analysis of Repeated Measurements

The multivariate analysis technique of repeated measures analysis was used to evaluate the effects of cohort and seed source on budworm performance data

and the effects of sample date and seed source on host foliage data. When repeated measurements (performance of insect cohorts and analysis of foliar constituents) are made on the same experimental unit (a tree) over time, the measurements tend to be correlated with each other. Use of an analysis technique that ignores this non-independence can result in a large Type I error (LaTour and Miniard 1983). Repeated measures analysis can be accomplished with either a univariate or a multivariate approach (Danford et al. 1960, Cole and Grizzle 1966, Winer 1971, Davidson 1972, Morrison 1976, LaTour and Miniard 1983).

Repeated measures analysis of data in this study was done using the multivariate approach provided by the GLM procedure of the SAS statistical computer system (SAS Institute, Inc. 1988). Individual tree values were used in all repeated measures analyses. For those variables having multiple observations per tree at each repeated measure (budworm weight, development time and growth rate) a mean value was computed for each tree. Seed source was the between-subjects effect. Budworm cohort or foliage sample date was the within-subject effect. The SAS procedure for repeated measures analysis provides multivariate test statistics such as Wilks' lambda criterion (Morrison 1976) for the repeated measure effect (cohort or sample date) and for the repeated measure x seed source interaction. F-values are computed from Wilks' lambda using Rao's (1973) procedure. The test for the between-subjects (seed source) effect is a univariate analysis of variance of tree sums (values for each tree are summed across all repeated measures).

Data from all eight budworm cohorts were included in repeated measures analysis of larval survival, but only cohorts 1 to 4 were included in the analyses of the other budworm performance variables that require data from surviving adults.

Because of greatly reduced larval survival in later cohorts, most trees did not have budworm adults in one or more of the last four cohorts.

Data from all 1986 samples of current-year foliage were used in repeated measures analysis of water content and leaf toughness. Only foliage samples collected from June to September in 1985 were used in repeated measures analysis of sugars, nitrogen and minerals. During budbreak and early shoot elongation in 1985 when small quantities of new foliage were available, sampling intensity was reduced to avoid removing large amounts of potential foliage from the study trees. Therefore, sugar, nitrogen and mineral data are not available for some trees, and in some cases one or two whole seed sources, for sample dates prior to 4 June.

Relationship of Host Susceptibility and Host Phenology

The relationship of host susceptibility to host phenology was examined by comparing the patterns in budworm performance data (1985) with the seasonal variation in foliar nutritional traits (1985 and 1986). The value of each foliar trait on each tree was determined for two points in the larval development of each budworm cohort: at 25% and 75% of the time required for post-overwintering larval development based on elapsed degree days during each cohort. Foliar values were determined at each of these two points for each cohort by interpolation of the foliar data from the two nearest foliar sample dates. The 25% and 75% points are roughly equivalent to the start of the 3rd larval stage and early 6th larval stage, respectively, based on the temperature and budworm development data presented by Regniere (1987). The 25% point therefore represents the time in development when most larvae in natural populations are moving from one-year-old foliage to expanding buds or new shoots. It also represents a point in post-overwintering development near which most mortality

occurs. The 75% point in development occurs near the start of the period of the greatest food consumption and weight gain.

Foliar values for early development (25% point) and late development (75% point) were combined with budworm performance data from each cohort to form an early development data set and a late development data set. Each data set consisted of 192 observations (8 cohorts X 24 trees). Relationships between budworm performance and foliar nutritional traits during early and late development were evaluated using canonical correlation analysis and regression techniques.

Canonical correlation analysis is a multivariate technique useful in analyzing the relationships between two sets of variables (insect performance variables and host quality variables) in a single procedure. Canonical correlation produces linear combinations (canonical variates) of the original variables in each data set that maximize the correlation between the two data sets. Interpretation of the results is done by examining the "loadings", i.e. the correlations of the original variables with the new canonical variates (Smith 1981, Sullivan and Moncreiff 1988). The relationships of budworm performance and host foliar quality were evaluated using the CANCORR procedure of the SAS system (SAS Institute, Inc. 1988) in separate analyses for early and late budworm development. Seed sources and budworm cohorts were pooled in each analysis. Observations with missing values for any variable were not included in the analysis procedure. Missing values occurred in some cases for budworm performance variables due to low larval survival in cohorts 5 to 8 or for foliar variables due to small foliage samples during budbreak and early shoot elongation. Therefore, 96 observations from cohorts 3 to 8 were used in the early development analysis, and 152 observations from all eight cohorts were used in the late development analysis. Canonical scores generated in the canonical correlation analysis were used in an

ordination procedure (Smith 1981) to map the insect performance-host quality relationships.

RESULTS

Phenological Window of Susceptibility

Relative Timing of Tree Phenology and Budworm Phenology

The relative timing of phenological events observed among the three white spruce seed sources in 1985 was consistent with the patterns observed in historical records for the white spruce provenance test. Bud expansion and budbreak occurred first in the SASK seed source and followed about one to two weeks later in the ONT and BC seed sources (Table 2). Budbreak had begun on some trees in the SASK seed source by Julian date (JD) 120 (equivalent to 234 elapsed degree days) and was nearly complete by JD 128 (309 degree days). Budbreak in the ONT seed source occurred during the following week (JD 128-135 and 309-421 degree days). Timing of budbreak in the BC seed source was similar to that of the ONT seed source, although 1/4 of the buds measured on the BC seed source did not break until after JD 135. These results are comparable to the timing of budbreak in early (228 degree days) and late-flushing clones (322 degree days) examined by Nienstaedt and King (1970).

Percent shoot elongation in the SASK seed source was one to two weeks ahead of that in the ONT and BC seed sources (Figure 1). The timing of shoot growth in the ONT and BC trees was similar, except that the ONT trees appeared to have a slightly longer growth period. By JD 135, shoot elongation was greater than 50% on SASK trees, but only 25% and 20% on ONT and BC trees,

Table 2. Bud phenology rating and percent of buds burst for three white spruce seed sources during April-May 1985 (N = 32 buds per seed source).

Julian Date	Accumulated Degree Days	Mean Bud Phenology Rating (± SE)			Percent of Buds Burst		
		SASK	ONT	BC	SASK	ONT	BC
114	182	2.2 (±0.1)	1.0 (±0.0)	1.0 (±0.0)	0.0	0.0	0.0
120	234	4.3 (±0.1)	3.0 (±0.0)	1.9 (±0.1)	34.4	0.0	0.0
128	309	5.8 (±0.1)	3.8 (±0.1)	3.1 (±0.1)	96.9	6.3	0.0
135	421	6.0 (±0.0)	5.9 (±0.1)	5.3 (±0.2)	100.0	96.9	75.0
142	481	6.0 (±0.0)	5.9 (±0.1)	6.0 (±0.0)	100.0	96.9	100.0
149	570	6.0 (±0.0)	6.0 (±0.0)	6.0 (±0.0)	100.0	100.0	100.0

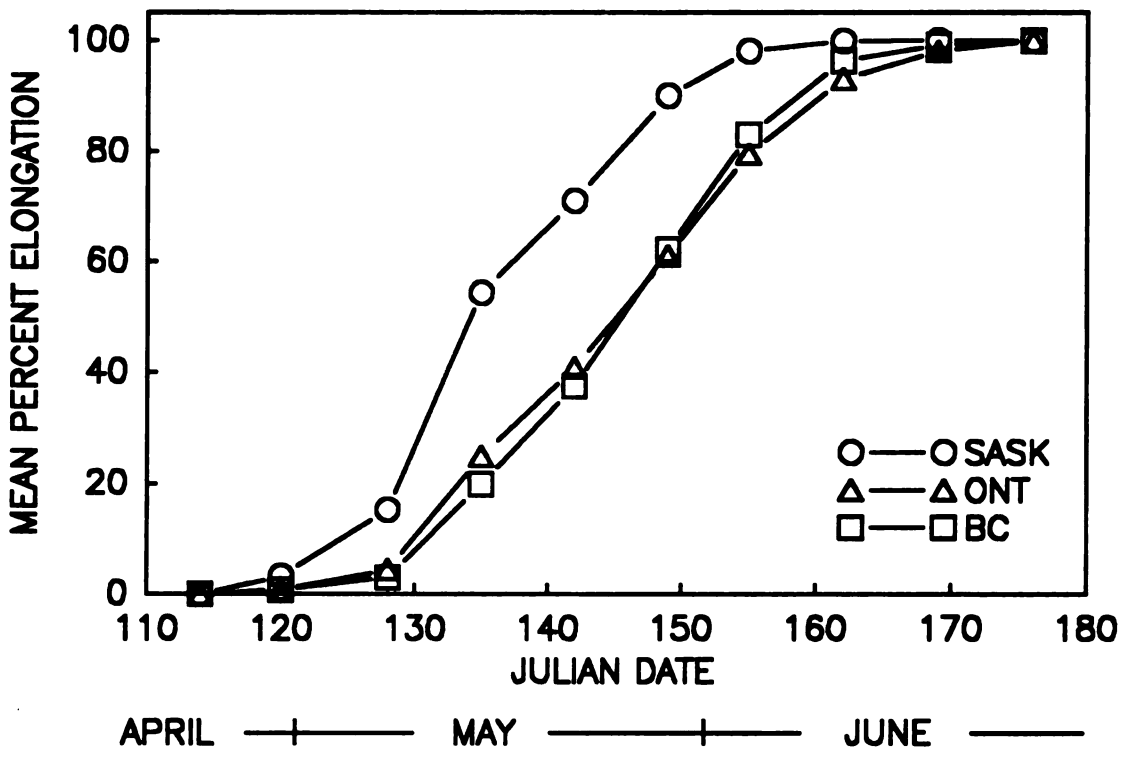

Figure 1. Shoot elongation of three white spruce seed sources in 1985.

respectively. Shoot elongation was completed on SASK, ONT and BC trees by JD 162, JD 176 and JD 169, respectively.

The timing of the placement of the eight spruce budworm cohorts on trees ranged from three weeks prior to budbreak to about one month after the completion of shoot growth (Figure 2). Cohort 1 was placed on the trees one to two weeks prior to budbreak in the early-flushing trees. Cohorts 2 and 3 started during the budbreak period. Cohort 4 started when new shoots were 50% elongated on the early-flushing trees, and buds were flushing on the late-flushing trees. Cohorts 5 and 6 started later in the shoot growth period, and cohorts 7 and 8 followed still later after the cessation of shoot growth. Only cohorts 1, 2 and 3 completed larval development prior to the end of the shoot growth period.

Spruce Budworm Performance

Budworm Cohorts and Tree Seed Sources -- Performance of the eight spruce budworm cohorts was measured by larval survival, pupal survival, adult weight, length of development period and growth rate. Larval survival averaged greater than 60% through the first three cohorts, but then substantially decreased to less than 35% in cohort 4 (Figure 3A). Larval survival further decreased to less than 10% in each of the last three cohorts. On some trees there were no survivors in the later cohorts, although this was true for only two of the 24 trees in the last three cohorts. At least some spruce budworms in each cohort were able to survive to pupation on each of the seed sources.

Pupal survival was generally high (> 75%) for all cohorts, but was highest (> 85%) for the later cohorts (Figure 3B). The increase in pupal survival later in the season may be partly due to the reduced sample size which resulted from low larval survival. However, it may reflect a reduced effect by natural enemies later in the season. Remarkably, parasitic ichneumonid wasps were able to sting and

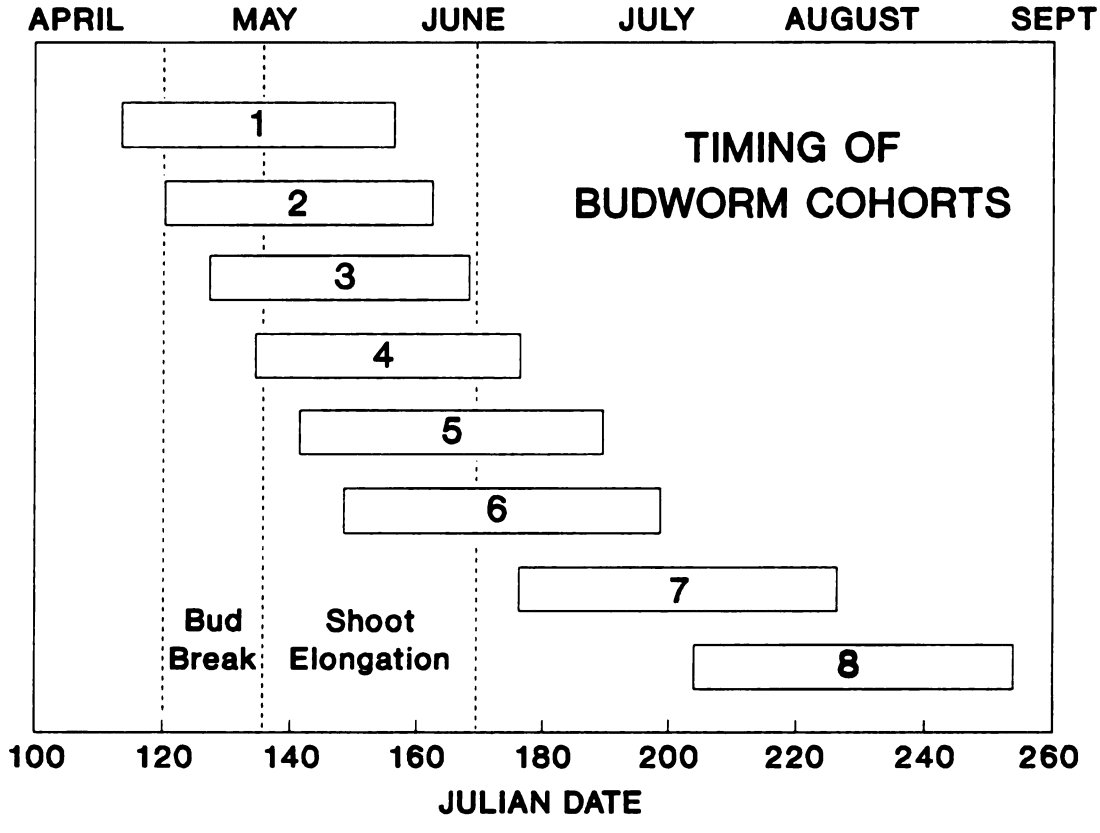

Figure 2. Relative timing of eight spruce budworm cohorts and white spruce budbreak and shoot elongation.

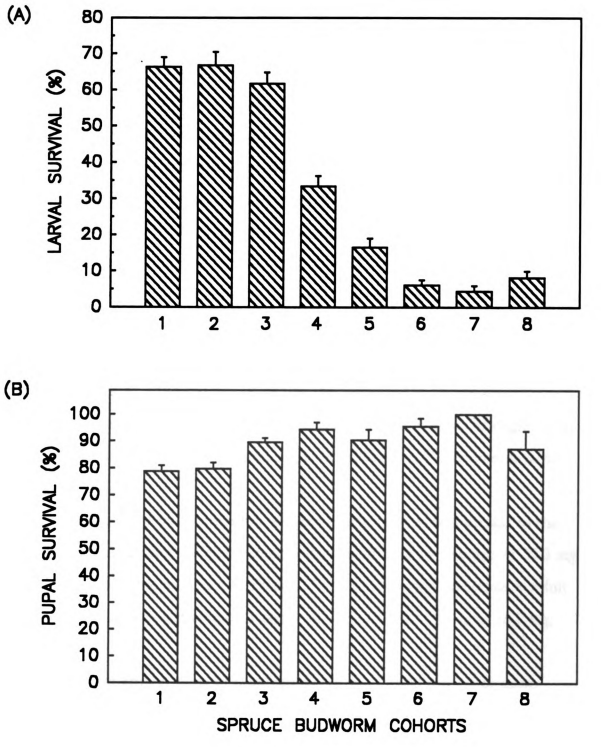

Figure 3. Mean percent survival (±SE) of (A) larvae and (B) pupae in eight spruce budworm cohorts.

parasitize budworms by inserting their ovipositors through the cloth surface of the branch cages. Parasitoids accounted for an average of 36%, 64% and 31% of pupal mortality in cohorts 1, 2 and 3, respectively. In cohorts 4 through 8, parasitoids emerged from only two budworm pupae.

The length of the development period from 2nd-stage larva to adult was measured both in number of calendar days and in degree days (Figure 4). Because development is temperature-dependent, development time measured in days is confounded by the effects of increasing temperatures as the growing season progressed. Degree days provide a unit of developmental time standardized across changing temperature regimes, and therefore allows more direct comparison of the effects of cohort timing on development. The number of days required for development was shallowly sigmoidal initially decreasing from 49.8 days (cohort 1) to 47.5 days (cohort 3) and then increasing to 55.2 days in cohort 6 (Figure 4). The number of degree days required for budworm development also was slightly sigmoidal, but generally the number of degree days increased continuously from 614 degree days in cohort 2 to 972 degree days in cohort 7 (Figure 4).

The pattern of budworm adult weights among cohorts was similar to the pattern of larval survival. Weights steadily decreased from an average of 26.0 mg in cohort 1 to 12.4 mg in cohort 8 (Figure 5A) with the largest decrease in adult weights occurring between cohorts 3 and 4, dropping from 23.7 mg to 16.7 mg, respectively.

Budworm growth rates were calculated as mg/degree day. The more common unit of measure, mg/day, can not be used, because of the confounding effect of increasing temperatures during the spring and summer. Budworm growth rates continually decreased from 0.042 mg/degree day in cohort 1 to 0.013 mg/degree day in cohort 8 (Figure 5B).

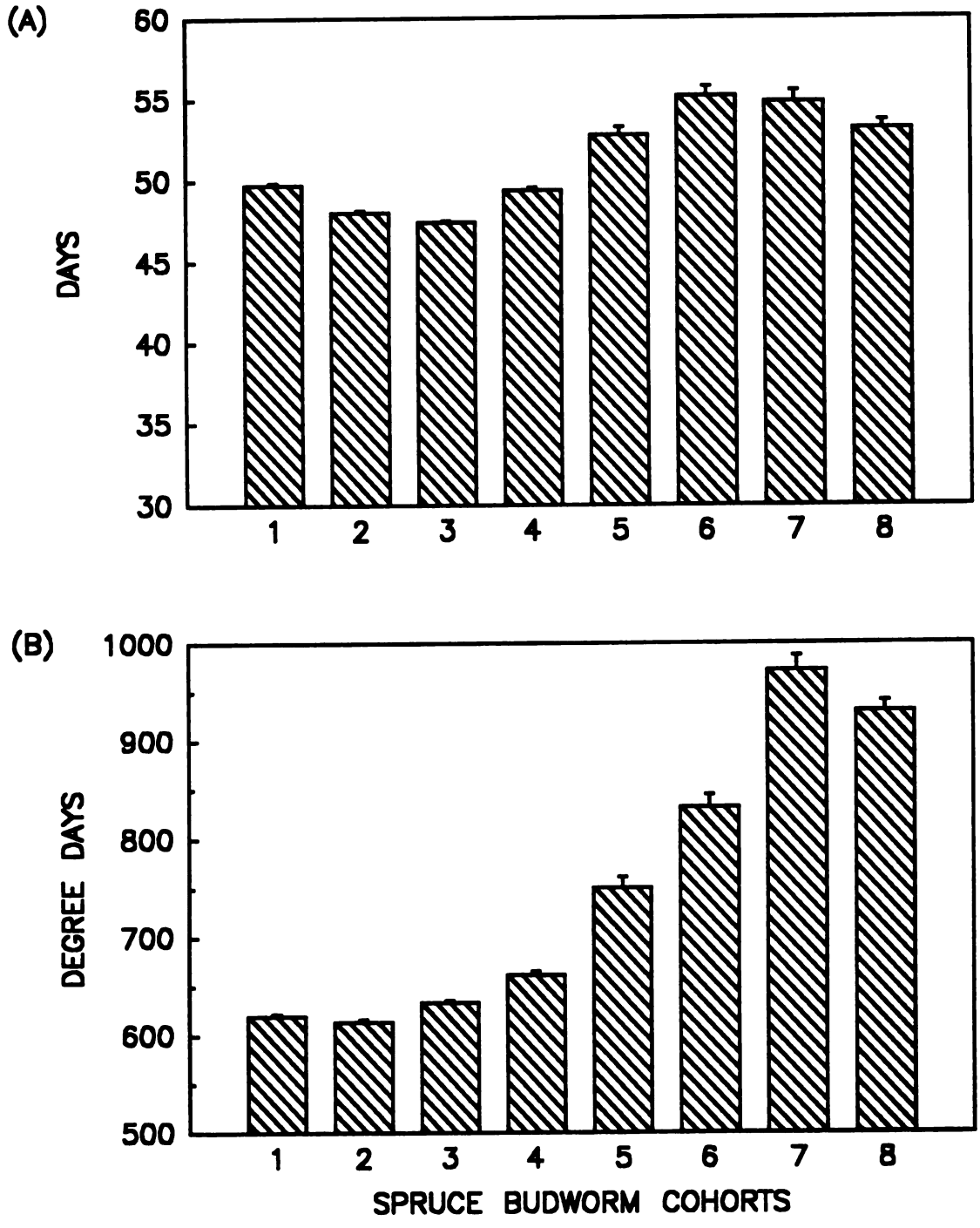

Figure 4. Mean length of development period (±SE) from second instar to adult measured in (A) days and (B) degree days for eight spruce budworm cohorts.

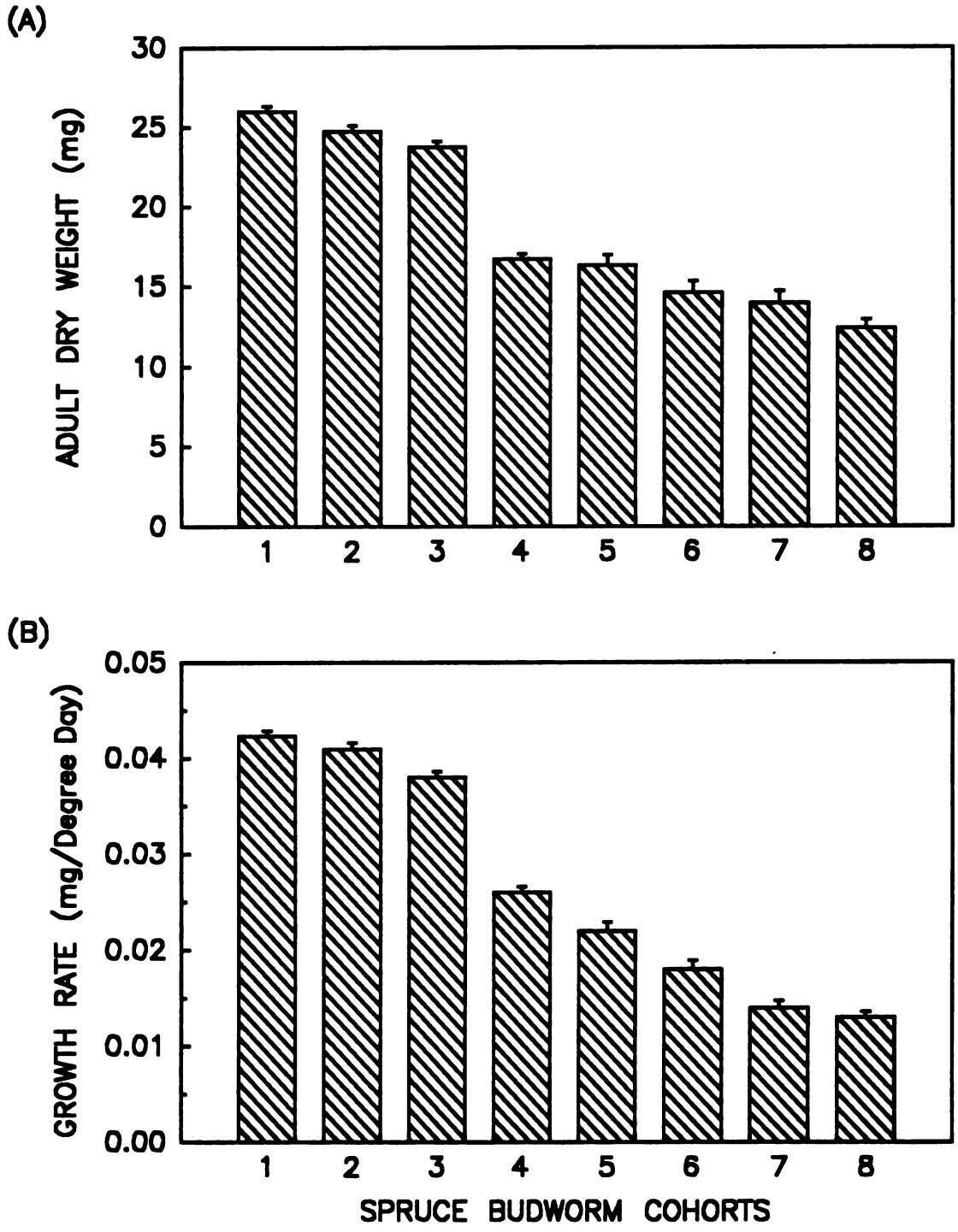

Figure 5. (A) Mean adult dry weight (±SE) and (B) mean growth rate (±SE) for eight spruce budworm cohorts.

A less direct measure of budworm performance in this study is the variation in defoliation levels. As would be expected with the declining larval survival, percent defoliation of current-year needles dropped sharply after the third cohort (Figure 6). Defoliation was generally highest on SASK trees and lowest on ONT trees. The effect of seed source on defoliation may be partially due to variation in timing of budbreak, but variation in shoot length and the quantity of foliage available are also important factors. The average shoot lengths (based on four mid-crown shoots/tree in 1985 and four mid-crown shoots/tree in 1986) of the SASK, ONT and BC trees were 11.9 cm, 16.9 cm and 13.4 cm, respectively. A significant ($P < 0.001$) negative relationship ($Y = 118.11 - 0.46\ X$, $r^2 = 0.34$) exists between percent defoliation (Y) and average shoot length per tree (X) for those early budworm cohorts (1, 2 and 3) that had high larval survival.

The effects of cohort timing and seed source on budworm performance were analyzed using repeated measures analysis. Cohort timing was a significant factor ($P < 0.001$) affecting all performance variables (Table 3). Seed source was a significant ($P \leq 0.05$) factor for all performance variables except pupal survival. The interaction between cohort and seed source was not significant ($P > 0.05$) for the survival variables, but was significant for length of development, adult weight and growth rate. Budworm performance within each cohort was generally lower (lower larval survival, adult weight and growth rate and longer development period) on the SASK seed source than on the other seed sources (Figures 7A, 8A, 9A and 10A). The same trends are evident when mean tree sums (sums of cohort values for each tree) are compared among seed sources (Table 4).

Seed Source Variation in Phenology -- One possible explanation for the reduced budworm performance on the SASK seed source is the more advanced phenology of these trees. As a test of this hypothesis, repeated measures analyses

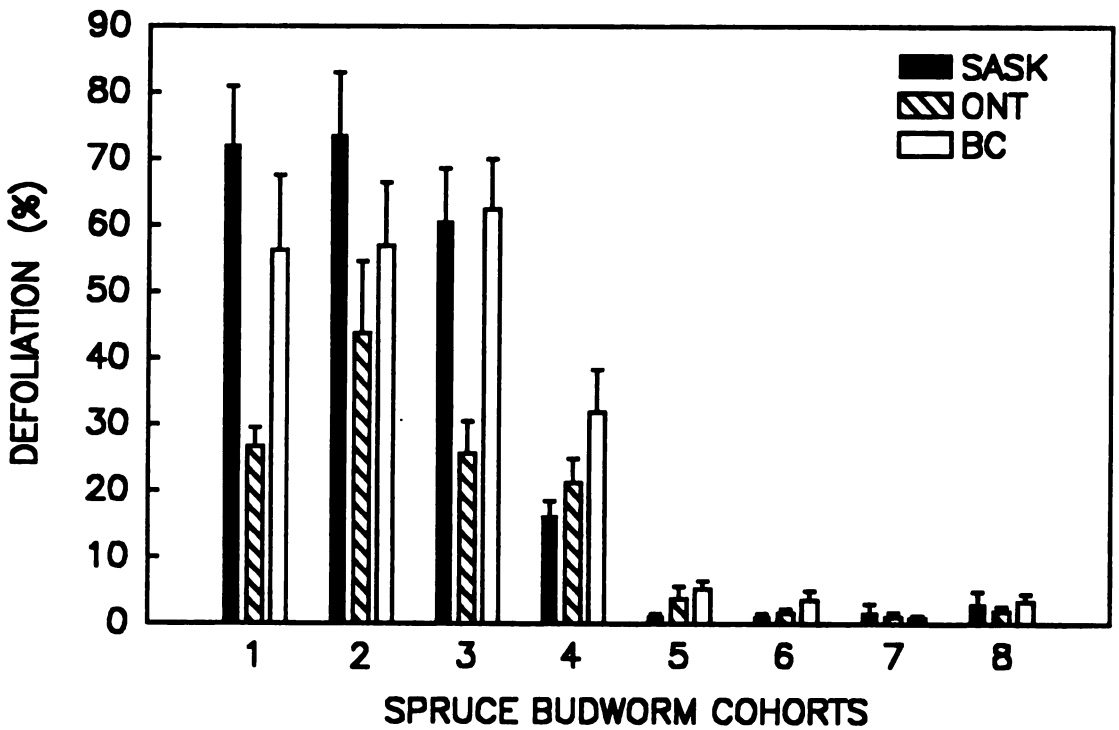

Figure 6. Mean percent defoliation (±SE) of current-year shoots for eight spruce budworm cohorts on three seed sources of white spruce.

Table 3. Multivariate repeated measures analysis of spruce budworm performance in 1985 with budworm cohorts as repeated measures.

Dependent Variable[1]	Source of Variation	Wilks' lambda[2]	F Value	Prob.
Cohorts 1-8:				
Larval Survival (%)	Cohort	0.0064	334.76	<0.001
	Cohort x Seed Source	0.2876	1.85	0.077
	Seed Source		5.64	0.011
Cohorts 1-4:				
Larval Survival (%)	Cohort	0.1458	37.10	<0.001
	Cohort x Seed Source	0.7258	1.10	0.380
	Seed Source		5.39	0.013
Pupal Survival (%)	Cohort	0.3441	12.07	<0.001
	Cohort x Seed Source	0.8056	0.73	0.634
	Seed Source		1.27	0.300
Length of Development (days)	Cohort	0.1377	39.65	<0.001
	Cohort x Seed Source	0.2808	5.62	<0.001
	Seed Source		7.27	0.004
Length of Development (degree days)	Cohort	0.3053	14.41	<0.001
	Cohort x Seed Source	0.3543	4.31	0.002
	Seed Source		6.72	0.006
Adult Dry Weight (mg)	Cohort	0.0659	89.84	<0.001
	Cohort x Seed Source	0.4679	2.93	0.019
	Seed Source		17.25	<0.001
Growth Rate (mg/degree day)	Cohort	0.0629	94.36	<0.001
	Cohort x Seed Source	0.3467	4.42	0.002
	Seed Source		19.23	<0.001

[1] Arcsine transformation performed on all survival data prior to analysis.

[2] Wilks' lambda criterion (Morrison 1976) used to compute F-values for cohort effect and cohort x seed source interaction using Rao's (1973) procedure.

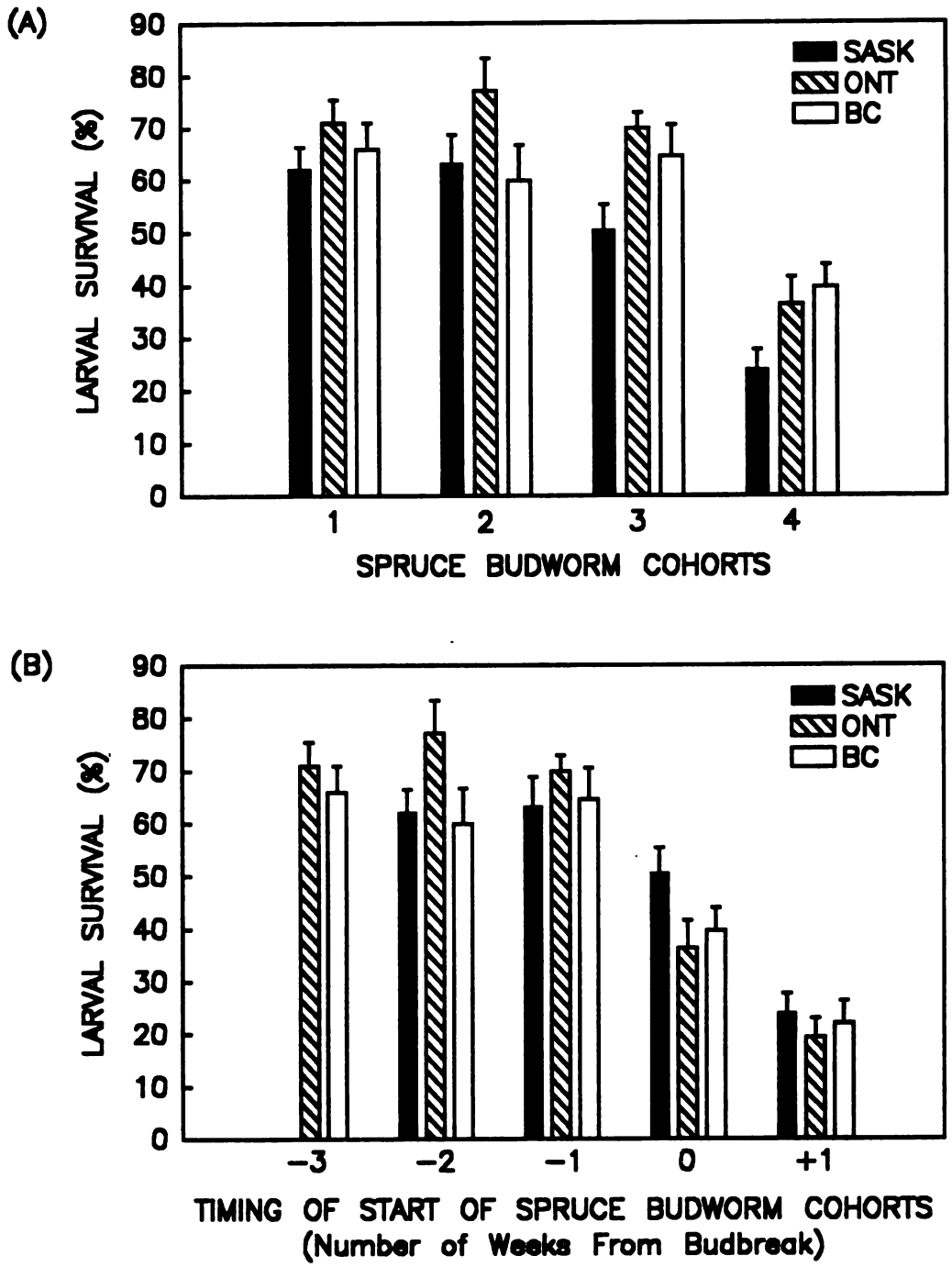

Figure 7. Mean percent larval survival (±SE) for (A) spruce budworm cohorts 1-4 on three white spruce seed sources and for (B) spruce budworm cohorts from phenologically similar host trees. Cohorts in (B) from weeks -3 and +1 were not used in repeated measures analyses but are presented for illustrative purposes only.

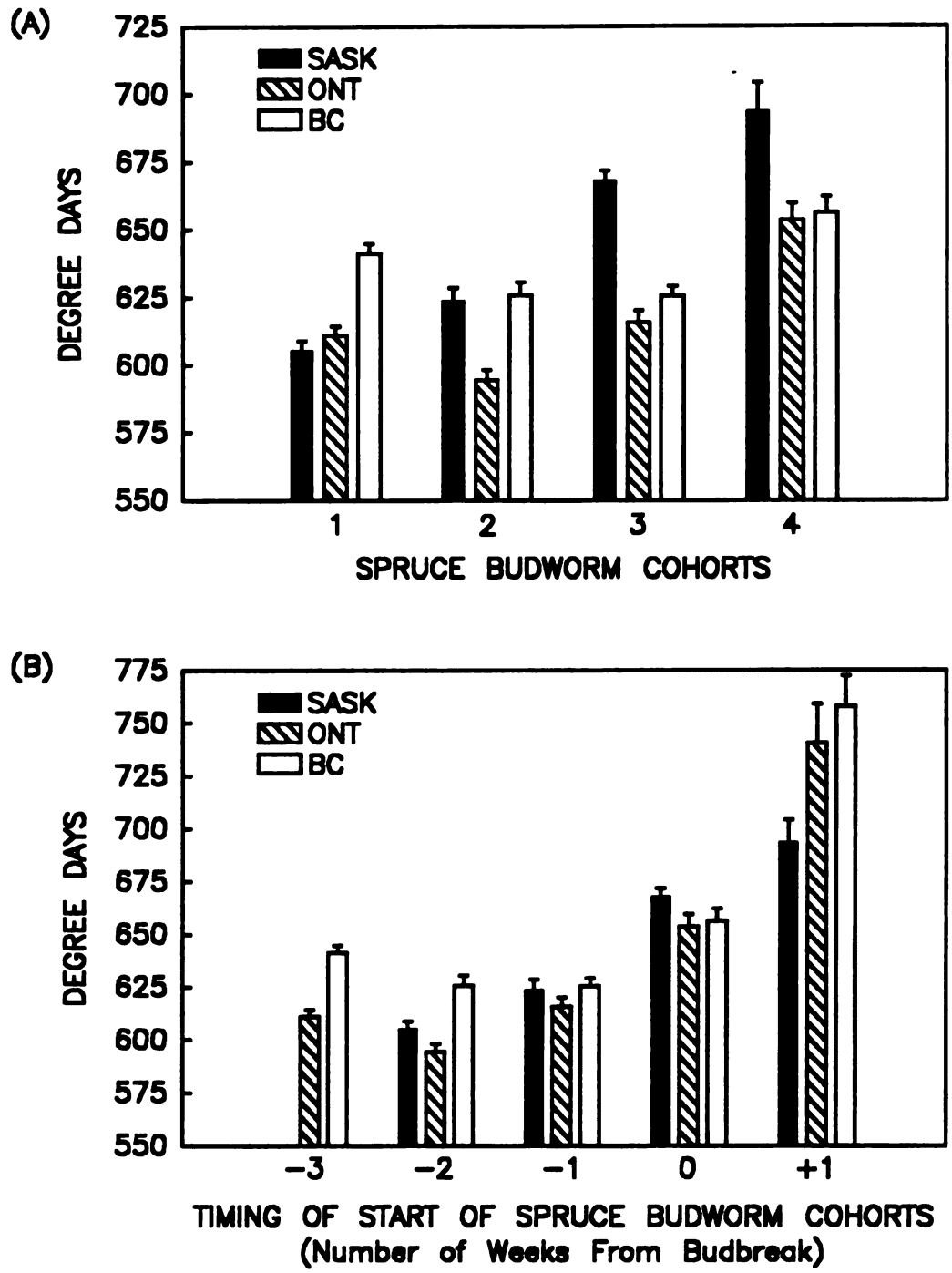

Figure 8. Mean length of development in degree days (±SE) for (A) spruce budworm cohorts 1-4 on three white spruce seed sources and for (B) spruce budworm cohorts from phenologically similar host trees. Cohorts in (B) from weeks -3 and +1 were not used in repeated measures analyses but are presented for illustrative purposes only.

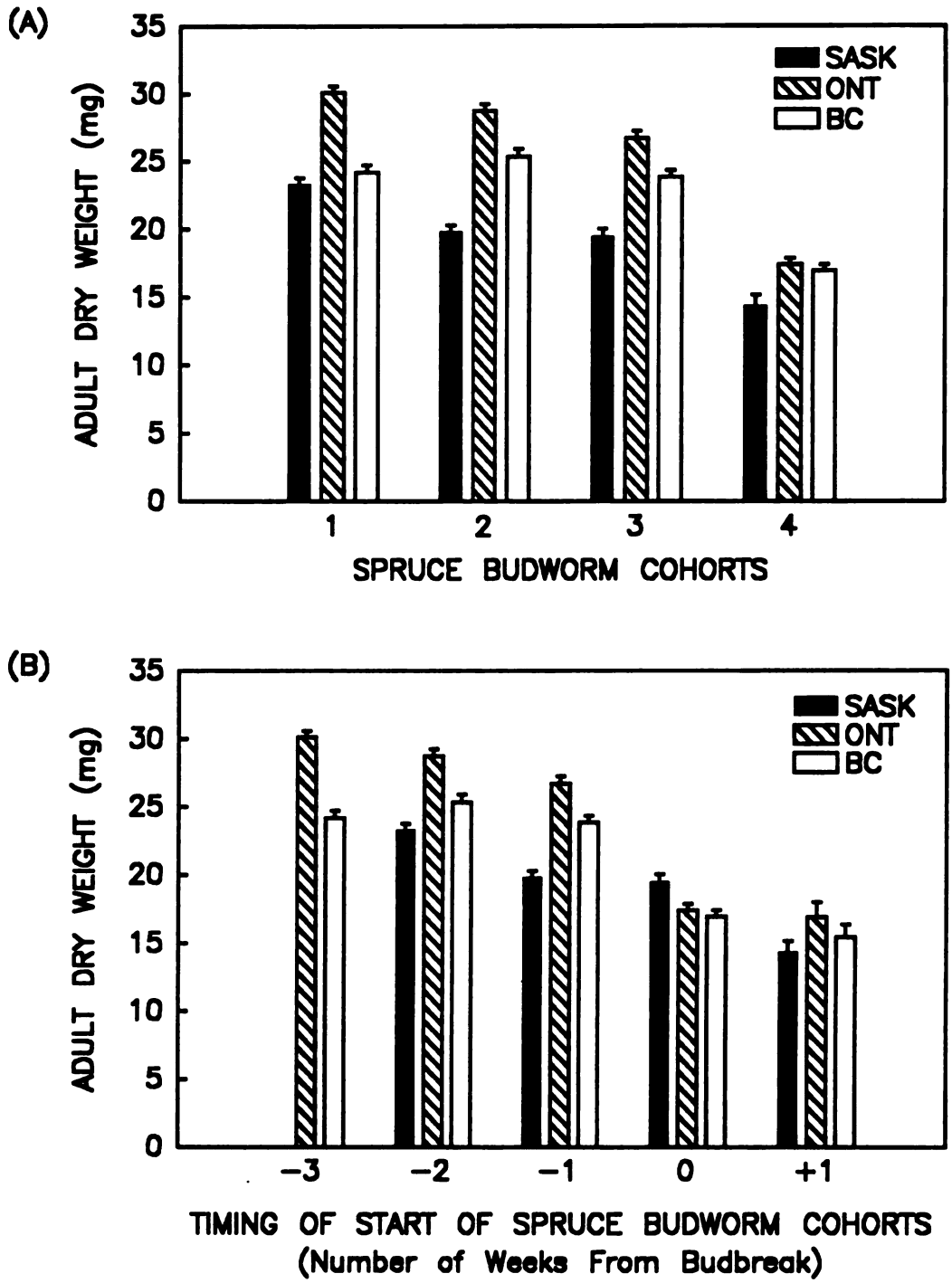

Figure 9. Mean adult dry weight (±SE) for (A) spruce budworm cohorts 1-4 on three white spruce seed sources and for (B) spruce budworm cohorts from phenologically similar host trees. Cohorts in (B) from weeks -3 and +1 were not used in repeated measures analyses but are presented for illustrative purposes only.

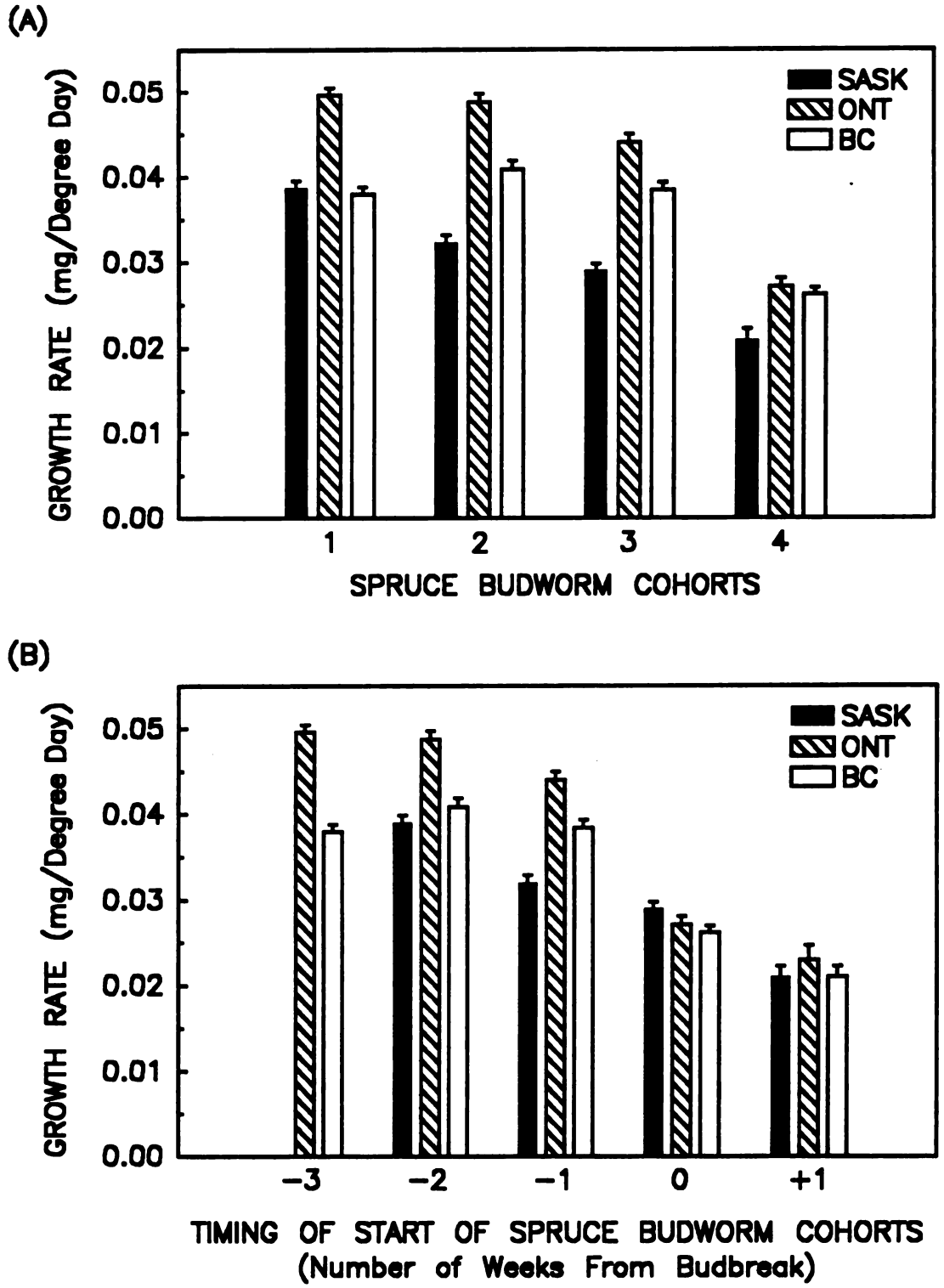

Figure 10. Mean growth rates (±SE) for (A) spruce budworm cohorts 1-4 on three white spruce seed sources and for (B) spruce budworm cohorts from phenologically similar host trees. Cohorts in (B) from weeks -3 and +1 were not used in repeated measures analyses but are presented for illustrative purposes only.

Table 4. Seed source effect on spruce budworm performance in 1985 represented as mean sums of cohort values for budworm performance variables.

Dependent Variable[1]	Mean Sums By Seed Source[2] SASK	ONT	BC
Cohorts 1-8:			
Larval Survival (%)	223.3 b	294.5 a	272.6 a
Cohorts 1-4:			
Larval Survival (%)	200.0 b	254.1 a	230.0 ab
Pupal Survival (%)	345.7 a	331.0 a	350.5 a
Length of Development (days)	197.5 a	192.2 b	196.4 a
Length of Development (degree days)	2599.8 a	2483.5 b	2549.5 ab
Adult Dry Weight (mg)	76.34 c	104.06 a	89.26 b
Growth Rate (mg/degree days)	0.120 c	0.171 a	0.142 b

[1] Arcsine transformation performed on all survival data prior to analysis.

[2] Cohort values are summed for each tree. Mean sum = mean of eight tree sums per seed source. Means within the same row followed by the same letter are not significantly different ($P > 0.05$, Tukey's Studentized Range Test).

were done using only equivalent cohorts from phenologically similar hosts. Budworm cohorts 1, 2 and 3 on SASK trees were reclassified as equivalent to cohorts 2, 3 and 4 on the ONT and BC trees (Figures 7B, 8B, 9B and 10B). This approach was used because the phenology of the SASK seed source was estimated to be about one week or more ahead of that of the ONT and BC seed sources, and cohorts 1 to 4 were started at one-week intervals. The combination of cohorts and seed sources used in this analysis represents three levels of insect-host synchrony -- i.e., budworm cohorts that were started at two weeks prior to budbreak, at one week prior to budbreak and at the same time as budbreak.

The seed source effect was no longer significant ($P > 0.05$) for larval survival and length of development (degree days) when phenologically similar hosts were used in the analyses (Tables 5 and 6). However, the seed source effect was still significant for adult weight and growth rate.

Tree Growth Rate -- Budworm performance was compared with tree growth rate to indicate how insect performance might be related to the relative vigor or growth characteristics of the host trees. Tree height varied among seed sources. The average heights at the end of the 1985 growing season were 3.0, 6.1 and 4.2 m for SASK, ONT and BC trees, respectively. Tree height growth rates averaged 11.0, 22.7 and 15.7 cm/yr, respectively. These averages are consistent with height data from the 14 plantations in the white spruce provenance study. Heights for SASK, ONT and BC trees have been approximately 70%, 130% and 80%, respectively, of plantation mean tree heights (Nienstaedt 1969, Wilkinson 1977b, Wright et al. 1977, Genys and Nienstaedt 1979).

Relationships of budworm performance to tree growth rate were analyzed with regression techniques. Seed sources were pooled and separate analyses were done on budworm cohorts from phenologically similar host trees, i.e., cohorts started two weeks prior to budbreak, cohorts started one week prior to budbreak

Table 5. Multivariate repeated measures analysis of spruce budworm performance in 1985 using cohorts from phenologically similar hosts (cohorts 1-3 of the SASK seed source and cohorts 2-4 of the ONT and BC seed sources) as repeated measures.

Dependent Variable[1]	Source of Variation	Wilks' lambda[2]	F Value	Prob.
Larval Survival (%)	Cohort	0.3194	21.31	<0.001
	Cohort x Seed Source	0.6643	2.27	0.079
	Seed Source		0.97	0.397
Pupal Survival (%)	Cohort	0.2789	25.86	<0.001
	Cohort x Seed Source	0.9485	0.27	0.897
	Seed Source		0.75	0.487
Length of Development (days)	Cohort	0.3048	22.80	<0.001
	Cohort x Seed Source	0.5867	3.06	0.028
	Seed Source		3.47	0.050
Length of Development (degree days)	Cohort	0.2565	28.99	<0.001
	Cohort x Seed Source	0.8124	1.09	0.372
	Seed Source		1.16	0.332
Adult Dry Weight (mg)	Cohort	0.1465	58.26	<0.001
	Cohort x Seed Source	0.3885	6.04	<0.001
	Seed Source		5.56	0.012
Growth Rate (mg/degree day)	Cohort	0.0808	113.82	<0.001
	Cohort x Seed Source	0.3593	6.68	<0.001
	Seed Source		6.03	0.008

[1] Arcsine transformation performed on all survival data prior to analysis.

[2] Wilks' lambda criterion (Morrison 1976) used to compute F-values for cohort effect and cohort x seed source interaction using Rao's (1973) procedure.

Table 6. Seed source effect on spruce budworm performance in 1985 using cohorts from phenologically similar hosts (cohorts 1-3 of SASK seed source and cohorts 2-4 of the ONT and BC seed sources). Seed source effect is represented as mean sums of cohort values for budworm performance variables.

Dependent Variable[1]	Mean Sums by Seed Source[2]		
	SASK	ONT	BC
Larval Survival (%)	176.0 a	183.2 a	164.2 a
Pupal Survival (%)	249.9 a	256.2 a	266.3 a
Length of Development (days)	146.4 a	143.1 b	145.0 ab
Length of Development (degree days)	1897.4 a	1869.0 a	1909.7 a
Adult Dry Weight (mg)	62.20 b	74.08 a	64.96 ab
Growth Rate (mg/degree days)	0.100 b	0.122 a	0.104 b

[1] Arcsine transformation performed on all survival data prior to analysis.

[2] Values of three cohorts are summed for each tree. Mean sum = mean of eight tree sums per seed source. Means within the same row followed by the same letter are not significantly different ($P > 0.05$, Tukey's Studentized Range Test).

and cohorts started during budbreak. Significant relationships ($P \leq 0.01$) between budworm performance and tree growth rate exist (Table 7) for those performance variables that were significantly affected by seed source even when only phenologically similar cohorts were used in analyses (Table 5). These relationships were present only in cohorts that started one or two weeks prior to budbreak. No significant relationships between budworm performance and tree growth rate were found for budworm cohorts that started at the time of budbreak. The length of budworm development in days for cohorts starting one or two weeks prior to budbreak was negatively related to tree growth rate (Figure 11). Adult weights and growth rates of these same insects were positively related to the growth rates of the trees (Figures 12 and 13). A weak relationship with tree growth rate also existed for larval survival of cohorts that started one week prior to budbreak.

Other Factors -- Further analyses were conducted to determine if factors other than phenological asynchrony and differences in tree phenology and growth rates may be confounding the observed cohort and seed source effects. Variation in insect vigor among batches of budworms received from the stock colony and seasonal variation in temperatures were examined as potential confounding factors of cohort effects.

Variation in performance among spruce budworm batches was minimal for insects reared in controlled conditions as part of laboratory feeding studies. Coefficients of variation (C.V.) were less than 10.0 for six of the seven performance variables measured (Tables 8 and 9). Spruce budworm performance in the field had a much higher level of variation (C.V. as high as 103.0) among budworm batches. This is the expected result for budworm batches placed on host trees at different points in the host phenology. The differences in performance values among batches in the field were in most cases 2 to 14 times

Table 7. Coefficients of determination (r^2) for the relationship of spruce budworm performance to tree growth rate (cm/yr) for budworm cohorts started at two weeks prior to budbreak, one week prior to budbreak and at budbreak in 1985.

Budworm Performance (Dependent Variable)	Timing of Start of Spruce Budworm Cohort		
	2 Weeks Prior to Budbreak	1 Week Prior to Budbreak	At Budbreak
Larval Survival (%)	0.15 n.s.	0.19 *	0.06 n.s.
Pupal Survival (%)	<0.01 n.s.	0.03 n.s.	<0.01 n.s.
Length of Development (days)	0.33 **	0.31 **	<0.01 n.s.
Length of Development (degree days)	0.10 n.s.	0.03 n.s.	0.02 n.s.
Adult Dry Weight (mg)	0.42 ***	0.56 ***	<0.01 n.s.
Insect Growth Rate (mg/degree day)	0.49 ***	0.49 ***	<0.01 n.s.

n.s., not significant; *, significant at $P \leq 0.05$; **, significant at $P \leq 0.01$; ***, significant at $P \leq 0.001$; for $Y = a + bX$ with X = tree growth rate (cm/yr).

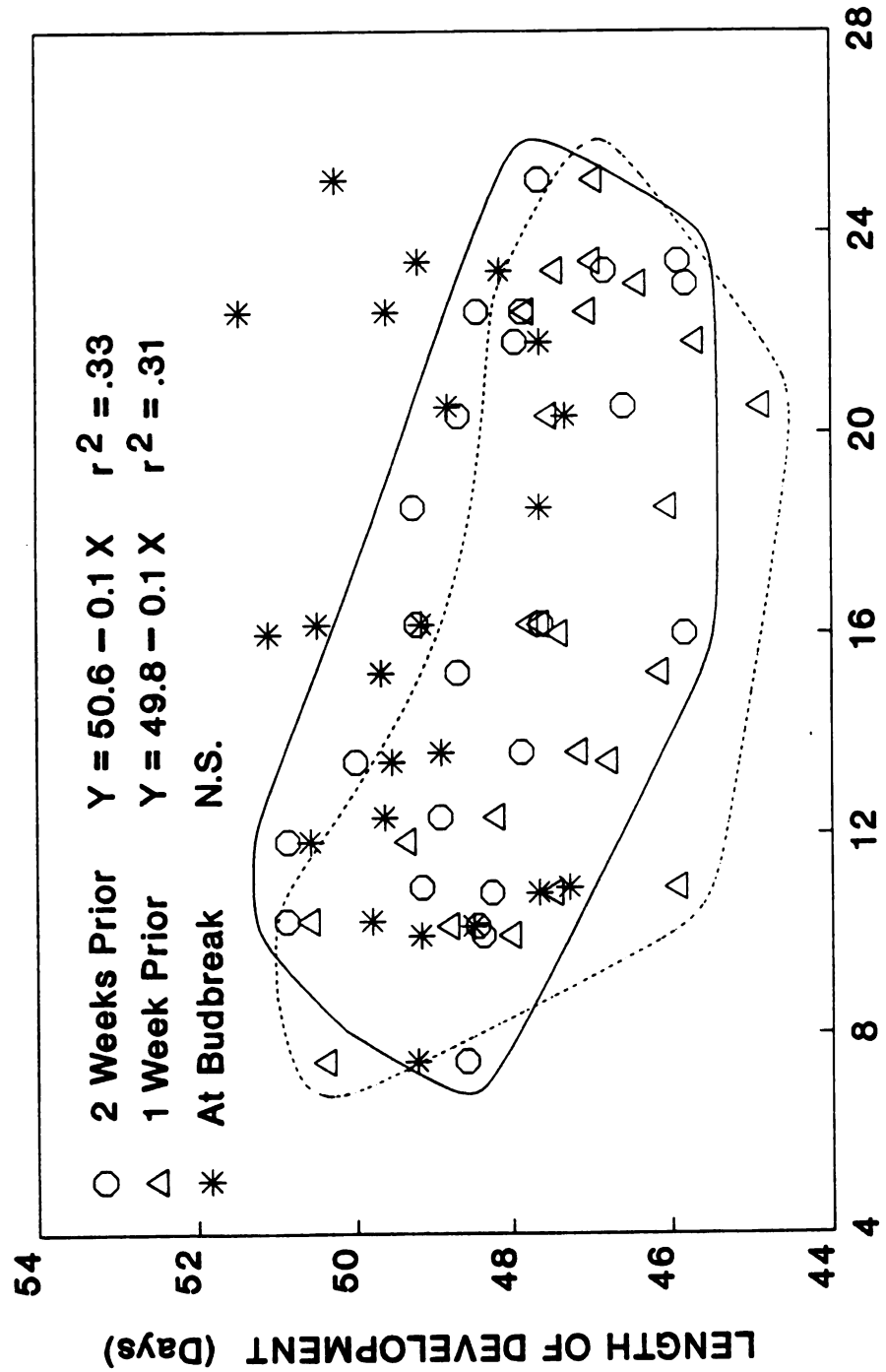

Figure 11. Relationship of length of development (days) of spruce budworms and host tree growth rate for budworm cohorts started two weeks prior (circles within solid line), one week prior (triangles within dashed line) and at budbreak (asterisks).

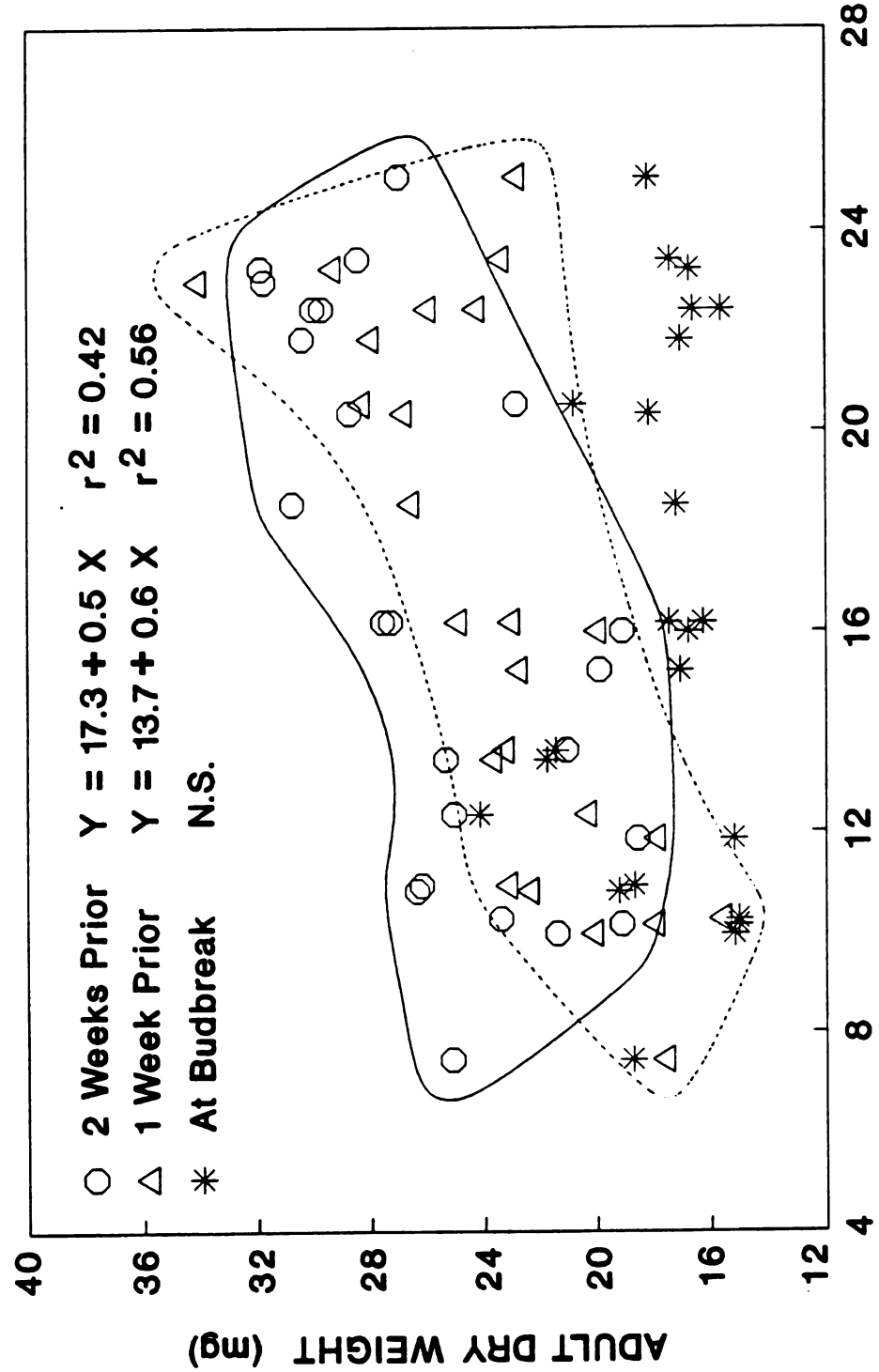

Figure 12. Relationship of spruce budworm adult dry weight and host tree growth rate for budworm cohorts started two weeks prior (circles within solid line), one week prior (triangles within dashed line) and at budbreak (asterisks).

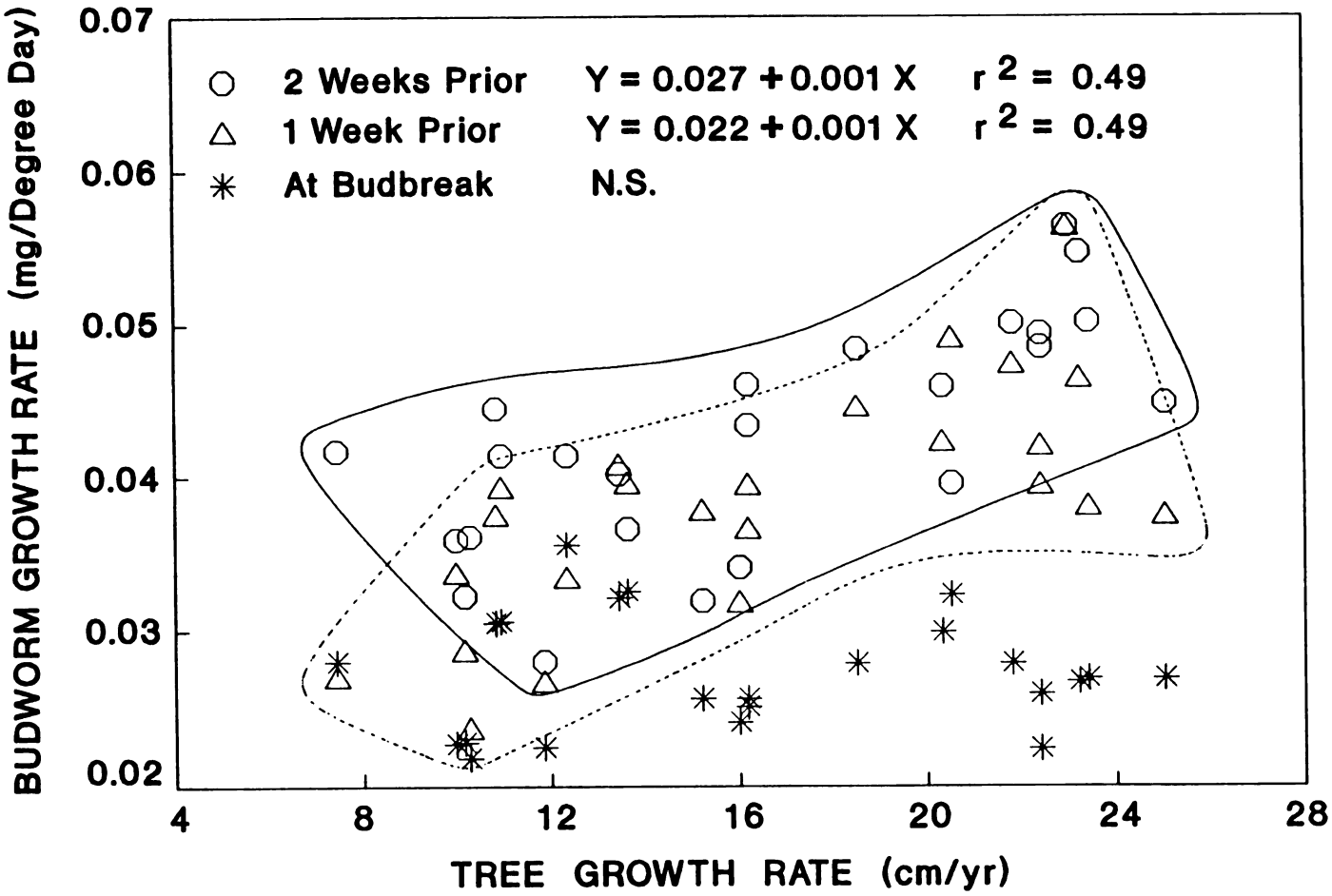

Figure 13. Relationship of spruce budworm growth rate and host tree growth rate for budworm cohorts started two weeks prior (circles within solid line), one week prior (triangles within dashed line) and at budbreak (asterisks).

Table 8. Comparison of spruce budworm survival rates among 1985 budworm batches for insects reared on artificial diet in laboratory studies and for insects in the white spruce field study.

	Batches Used in Laboratory Studies[1]					
	January	March	June[2]	November	Mean ± SD	C.V.
No. Insects	400	400	200	400		
Survival (%)						
Larvae	70.5	71.3	--	63.8	68.5 ± 4.2	6.1
Pupae	82.5	78.8	--	94.9	85.4 ± 8.4	9.8
Total	58.2	56.2	69.0	60.5	61.0 ± 5.6	9.2

	Batches Used in Field Study[3]				
	April Cohorts 1-3	May Cohorts 4-6	June Cohorts 7-8	Mean ± SD	C.V.
No. Insects	2180	1445	1120		
Survival (%)					
Larvae	64.9	18.7	6.3	30.0 ± 30.9	103.0
Pupae	82.7	93.3	91.8	89.2 ± 5.7	6.4
Total	53.3	17.6	5.8	25.6 ± 24.7	96.5

[1] Values for laboratory studies are based on one observation per batch.

[2] Data for larval and pupal survival not available for June batch in laboratory study.

[3] Values for field study are averages based on 72, 71 and 47 caged branches, respectively, for the three batches.

Table 9. Comparison of spruce budworm length of development, adult weight and growth rate among 1985 budworm batches for insects reared on artificial diet in laboratory studies and for insects in the white spruce field study.

	Batches Used in Laboratory Studies					
	Jan.	March	June	Nov.	Mean ± SD	C.V.
No. Insects	233	218	138	242		
Length of Development[1] (days)	40.5	35.8	41.5	38.6	39.1 ± 2.5	6.5
Length of Development (degree days)	666.6	588.1	682.6	634.2	642.9 ± 41.7	6.5
Adult Dry Weight (mg)	23.20	27.04	23.29	21.62	23.79 ± 2.30	9.7
Growth Rate (mg/degree day)	0.035	0.047	0.035	0.035	0.038 ± 0.006	15.6

	Batches Used in Field Study				
	April Cohorts 1-3	May Cohorts 4-6	June Cohorts 7-8	Mean ± SD	C.V.
No. Insects	1111	230	64		
Length of Development[1] (days)	48.5	50.7	53.7	51.0 ± 2.6	5.1
Length of Development (degree days)	622.3	698.5	944.2	755.0 ± 168.2	22.3
Adult Dry Weight (mg)	24.85	16.40	12.90	18.05 ± 6.14	34.0
Growth Rate (mg/degree day)	0.040	0.024	0.014	0.026 ± 0.013	50.0

[1] Batch values for each insect performance variable are averages of individual insect values.

as great as the standard deviation among batches in the laboratory studies. Thus, differences among budworm batches in field tests were assumed to be due to causes other than variation among stock colony batches. Pupal survival was the only performance variable that had very small differences among batches in the field (differences < 1.5 times the standard deviation in the laboratory). An interesting point in these comparisons of laboratory and field-reared insects is that the performance values for the first budworm batch in the field (cohorts 1 to 3 -- i.e., those insects that were most closely synchronized with tree phenology) were quite similar to the mean performance values for the laboratory-reared insects.

Repeated measures analysis of field temperature data revealed that the daily average temperature, daily maximum temperature and number of degree days per day did not differ significantly ($P > 0.05$) among cohorts 1 to 4 (Table 10). However, when cohorts 5 through 8 were added incrementally to the analysis, there was in each case a significant difference among cohorts for each of the three temperature variables. Daily maximum temperatures greater than 30 °C occurred only once prior to 1 July (JD 182). During the period in which cohort 7 was on the trees (JD 176-226), 17 of 50 days had maximum temperatures greater than 30 °C. However, no temperatures greater than 33.5 °C were recorded during the course of this study. Higher temperatures later in the season are not considered to be a serious confounding factor, because they were present several weeks after the major changes in budworm performance occurred.

Spruce Budworm Survivorship Curve

The pattern of the spruce budworm survivorship curves is the same for both early (April-June) and late (June-July) cohorts in the 1987 survivorship experiment (Figure 14). More than 85% of the total larval mortality occurred by

Table 10. Daily average temperatures, daily maximum temperatures and degree days per day during the period that eight spruce budworm cohorts were caged on white spruce in 1985.

Cohort	# Days in Field	Daily Average Temp. (°C) Mean	S.E.	Daily Maximum Temp. (°C) Mean	S.E.	Degree Days Per Day Mean	S.E.
1	45	13.3	± 0.58	22.8	± 0.61	11.3	± 0.55
2	43	13.7	± 0.58	23.3	± 0.61	11.6	± 0.54
3	42	14.0	± 0.59	23.4	± 0.64	12.0	± 0.57
4	43	13.9	± 0.52	23.2	± 0.62	11.8	± 0.51
5	49	15.4	± 0.55	24.8	± 0.59	13.3	± 0.52
6	51	16.4	± 0.57	25.6	± 0.60	14.2	± 0.55
7	51	19.3	± 0.40	28.1	± 0.43	17.1	± 0.38
8	50	19.0	± 0.42	25.5	± 0.53	17.0	± 0.41

Cohort Effect[1]	F Value	Prob.	F Value	Prob.	F Value	Prob.
Cohorts 1-4	0.49	0.688	0.21	0.886	0.51	0.677
Cohorts 1-5	3.81	0.011	2.71	0.045	4.32	0.006
Cohorts 1-8	28.91	<0.001	13.93	<0.001	31.88	<0.001

[1] Repeated measures analysis using cohorts as repeated measures.

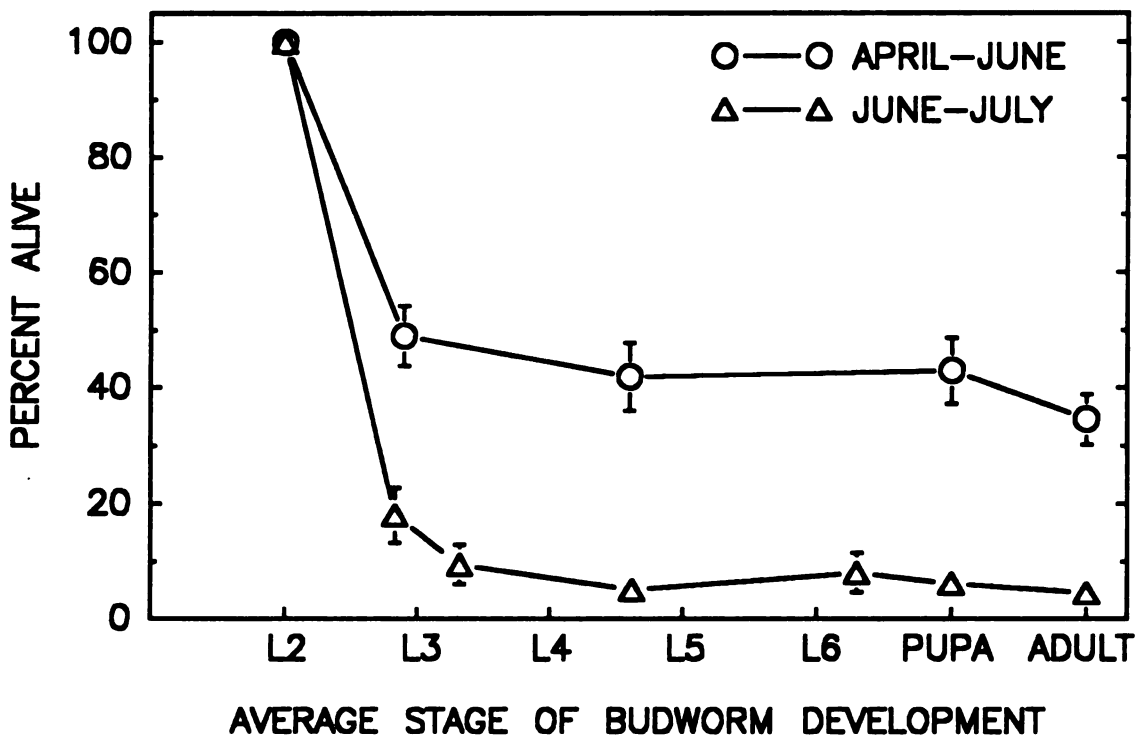

Figure 14. Spruce budworm survivorship curves (mean percent alive ± SE) for an early cohort (April-June) and a late cohort (June-July) on the ONT seed source during 1987.

the time most budworms had become 3rd instars, thus demonstrating a "type A" survivorship curve (sensu Price 1984). These results are comparable to the survivorship curve developed by Morris and Miller (1954) for field populations of spruce budworms.

The trends in budworm performance in this 1987 experiment agree with the results of the 1985 experiment. Larval survival and adult weight were much higher and the degree days required for development were much fewer in the early cohort than in the late cohort (Table 11). Larval survival in the early cohort in 1987 (43%) was, however, about one-third less than larval survival in the first three cohorts in 1985 (Figure 3A). This may be partly due to the earlier start of the first cohort in 1987, which caused the young budworm larvae to be on the trees for one to two weeks longer prior to budbreak than were larvae of the first cohort in 1985. The early cohort in 1987 was placed on the trees at 40 fewer accumulated degree days (133 vs 173) and at one to two weeks earlier in terms of host phenology (four to five weeks vs three weeks prior to budbreak on ONT trees) than cohort 1 in 1985. However, peak pupation occurred at ca. 85% shoot elongation for both the early cohort in 1987 and cohort 1 in 1985.

The timing of the late cohort in 1987 was slightly later than that of the sixth cohort in 1985. The late cohort in 1987 was placed on the trees at ca. 90% shoot elongation. Cohort 6 in 1985 was started at ca. 60% shoot elongation. Peak pupation occurred at ca. three weeks after the end of the shoot growth period for both the late cohort in 1987 and cohort 6 in 1985.

The within-branch locations of the budworm larvae were recorded during branch examination in 1987 as an indication of larval feeding sites (Table 12). Prior to budbreak, most 2nd and 3rd-stage larvae of the April-June cohort were either mining the previous year's needles or were situated in webbing among the

Table 11. Spruce budworm performance for the two budworm cohorts in the 1987 survivorship experiment.

Budworm Performance	April-June Cohort N	April-June Cohort Mean (±SE)	June-July Cohort N	June-July Cohort Mean (±SE)
Larval Survival (%)	10	43.0 (±5.8)	10	6.2 (± 1.8)
Pupal Survival (%)	10	84.2 (±5.6)	7	81.0 (±14.3)
Adult Dry Weight (mg)	77	30.9 (±0.7)	10	13.8 (± 1.2)
	N	Median[1]	N	Median
Length of Development (days)	77	61.0	10	47.9
Length of Development (degree days)	77	780.5	10	905.2

[1] Median values are given for length of development because more than one-third of surviving insects in the April-June cohort had completed development prior to the time of final branch examination.

Table 12. Average larval stage and distribution of spruce budworm larvae on caged branches in relation to timing of budbreak during the 1987 survivorship experiment.

	April-June Cohort		June-July Cohort			
	Number of Weeks Prior to Budbreak		Number of Weeks After Budbreak			
	-1	0	+4	+5	+6	+7
Average Larval Stage[1]	2.9	4.6	2.8	3.3	4.6	6.0
Total Number Larvae	102	93	50	24	13	16
Percent of Total Larvae By Location on Branch:						
Old Needles -- Mines	14.7	1.1	2.0	0.0	0.0	0.0
Old Needles -- External	39.2	10.7	0.0	0.0	0.0	0.0
Vegetative Buds[2]	40.2	64.5	---	---	---	---
New Needles -- Mines	---	---	22.0	16.7	0.0	0.0
New Needles -- External	---	---	54.0	50.0	76.9	81.2
Moving or Not On Branch	5.9	23.7	22.0	33.3	23.1	18.8

[1] Average instar number

[2] Vegetative buds were present only during the April-June cohort. Expanded shoots with new needles were present only during the June-July cohort.

bases of those needles. As the vegetative buds became swollen, more larvae were located next to or within the buds. After budbreak the older larvae fed primarily on foliage of the newly expanding shoots.

Larvae of the June-July cohort were rarely found on or in the previous year's foliage (Table 12). Almost all of the needle mining done by young larvae in this cohort occurred in the new needles of the expanding shoots. As the larvae matured they continued feeding almost exclusively on new foliage.

Larval counts from the first two sample dates of the early cohort were lower than all later larval counts in that cohort. Apparently many larvae were not detected during those early branch examinations because of the extreme difficulty of finding the smallest 2nd instars as they mined old needles and vegetative buds. Data from these two dates have not been included in Figure 14 and Table 12. This problem did not exist in the late cohort, because buds were not present at that time, and due to warmer temperatures most larvae that were alive at the first sample date were more easily found because they were larger 3rd instars.

Seasonal Variation in Host Nutritional Traits

The timing of budbreak and shoot growth phenology were very similar for 1985 and 1986. Budbreak in the early-flushing SASK seed source occurred between 28 April and 8 May, or at 200-300 accumulated degree days in both years. Fifty percent shoot elongation on SASK trees occurred at ca. 13-14 May and 400-410 degree days in both years. The same between-year similarities occurred for ONT and BC trees, however the timing of phenological events in these seed sources was 7-10 days and 100-125 degree days later than that of the SASK seed source.

Current-Year Foliage

All measured nutritional traits in current-year foliage varied significantly ($P \leq 0.001$) among sample dates (Table 13). For most of these traits the greatest quantitative changes occurred during the period of active shoot growth. A seed source effect and a sample date x seed source interaction were also significant ($P \leq 0.05$) for several traits (Table 13). Mean sums of repeated measurements were used to compare individual seed sources (Table 14).

Sugars -- Total foliar sugar (fructose + glucose + sucrose) in new foliage was at its highest levels near the middle of the shoot elongation period and then generally decreased during the summer months (Figure 15). The earliest sample date for which sufficient foliage was available for sugar analyses was 17 May (JD 137). The highest total sugar levels observed on SASK trees (15.0%) occurred on that date. SASK trees at that time had reached 60% shoot elongation. ONT trees had reached 30% shoot elongation at that time and had a total sugar level of 14.4%. Twelve days later at about 60% shoot elongation the total sugar level in ONT trees peaked at 15.5%. This difference in the timing of the peak levels of total sugar may be the result of the difference in timing of phenology between the SASK and ONT seed sources. However, the pattern does not appear to hold for the late-flushing BC seed source which has a trend similar to that of the early-flushing SASK seed source.

Nitrogen and Minerals -- Total nitrogen and phosphorous levels in current-year foliage were highest in the swelling buds, declined rapidly at the time of budbreak, and then remained low through the summer (Figure 16). Prior to budbreak, ONT trees had the highest levels of both nitrogen and phosphorous. However, the slightly lower levels in SASK trees may be due to the advanced phenology of that seed source. Data for the first sample date (1 May) are based on a sub-sample of trees (three trees each for SASK and ONT sources and one

Table 13. Multivariate repeated measures analysis of total sugar, total nitrogen and mineral content of current-year foliage in June-September 1985 and water content and toughness of current-year foliage in May-August 1986 with sample dates as repeated measures.

Dependent Variable	Source of Variation	Wilks' lambda[1]	F Value	Prob.
Total Sugar	Date	0.1818	15.30	<0.001
	Date x seed source	0.4121	1.90	0.080
	Seed source		1.97	0.165
Nitrogen	Date	0.2524	131.30	<0.001
	Date x seed source	0.1898	4.40	<0.001
	Seed source		2.67	0.093
Phosphorous	Date	0.0266	124.58	<0.001
	Date x seed source	0.2833	2.99	0.008
	Seed source		11.79	<0.001
Potassium	Date	0.0278	118.94	<0.001
	Date x seed source	0.3555	2.30	0.034
	Seed source		3.53	0.048
Calcium	Date	0.0549	58.53	<0.001
	Date x seed source	0.4068	1.93	0.075
	Seed source		1.05	0.368
Magnesium	Date	0.0777	40.34	<0.001
	Date x seed source	0.2997	2.81	0.012
	Seed source		1.80	0.190
Manganese	Date	0.1141	26.40	<0.001
	Date x seed source	0.1530	5.29	<0.001
	Seed source		8.80	0.002
Copper	Date	0.1097	27.58	<0.001
	Date x seed source	0.6150	0.94	0.514
	Seed source		3.47	0.050
Iron	Date	0.2999	7.94	<0.001
	Date x seed source	0.3751	2.15	0.047
	Seed source		3.59	0.046
Sodium	Date	0.1859	14.89	<0.001
	Date x seed source	0.5124	1.35	0.245
	Seed source		1.95	0.167

Table 13 (cont'd.).

Dependent Variable	Source of Variation	Wilks' lambda[1]	F Value	Prob.
Zinc	Date	0.1660	17.09	<0.001
	Date x seed source	0.3397	2.43	0.026
	Seed source		1.53	0.239
Water Content	Date	0.0044	1009.45	<0.001
	Date x seed source	0.0402	17.94	<0.001
	Seed source		6.58	0.006
Toughness	Date	0.0072	623.22	<0.001
	Date x seed source	0.0727	12.19	<0.001
	Seed source		1.93	0.170

[1] Wilks' lambda criterion (Morrison 1976) was used to compute F-values for date effect and date x seed source interaction using Rao's (1973) procedure.

Table 14. Seed source effects on foliar characteristics represented as mean sums of repeated measurements for current-year foliage variables.

Foliar Trait	Units	Mean Sums By Seed Source[1]		
		SASK	ONT	BC
Total Sugar	% dw	63.2 a	69.5 a	68.1 a
Nitrogen	% dw	7.38 a	7.44 a	7.99 a
Phosphorous	mg/g dw	10.46 a	10.67 a	12.82 b
Potassium	mg/g dw	54.30 a	60.23 ab	66.47 b
Calcium	mg/g dw	20.93 a	20.17 a	18.17 a
Magnesium	mg/g dw	6.61 a	7.11 a	7.12 a
Manganese	mg/g dw	2.92 a	3.83 ab	4.76 b
Copper	μg/g dw	27.8 a	31.9 a	32.6 a
Iron	μg/g dw	239.6 a	195.2 b	203.8 ab
Sodium	μg/g dw	171.0 a	177.6 a	195.6 a
Zinc	μg/g dw	260.3 a	278.3 a	240.6 a
Water Content	% fw	332.1 a	340.2 b	336.6 ab
Toughness	g	2878.8 a	3095.4 a	2817.2 a

[1] Sum of repeated measurements = sum of six sample dates (total sugar, total nitrogen and minerals in June-September 1985) or five sample dates (water content and toughness in May-August 1986) per tree.

N = 8 trees for each mean. Means within the same row followed by the same letter are not significantly different ($P > 0.05$, Tukey's Studentized Range Test).

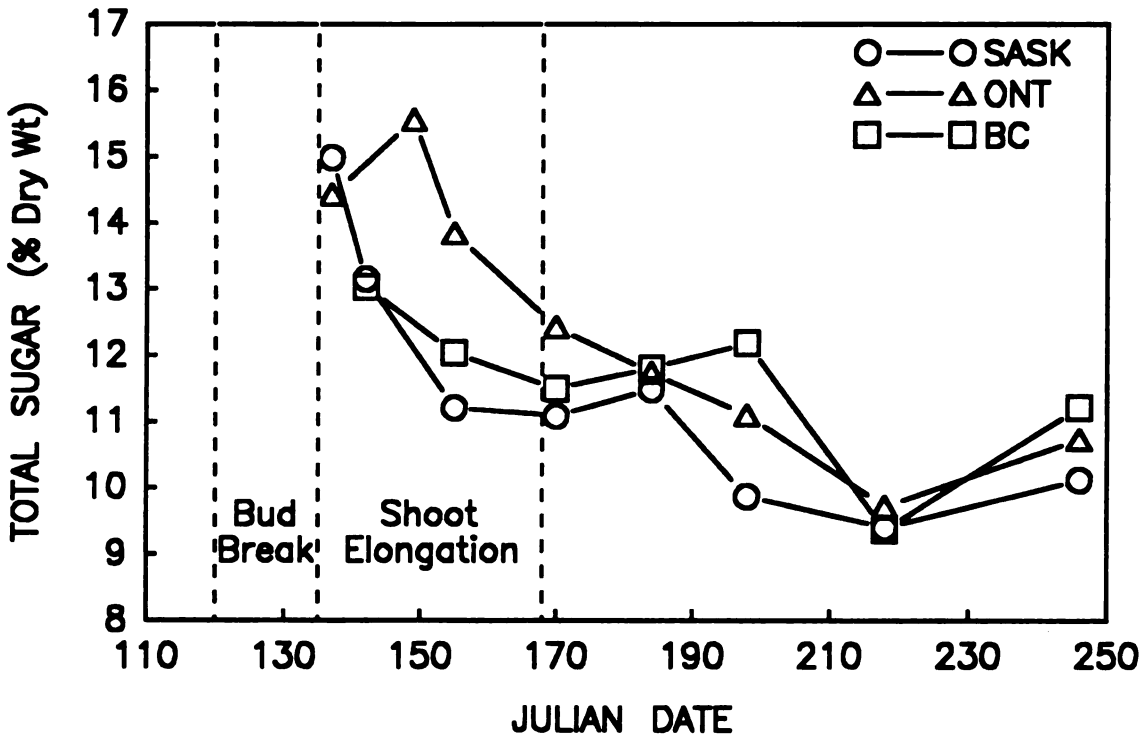

Figure 15. Seasonal variation of total sugar in current-year foliage of three seed sources in 1985.

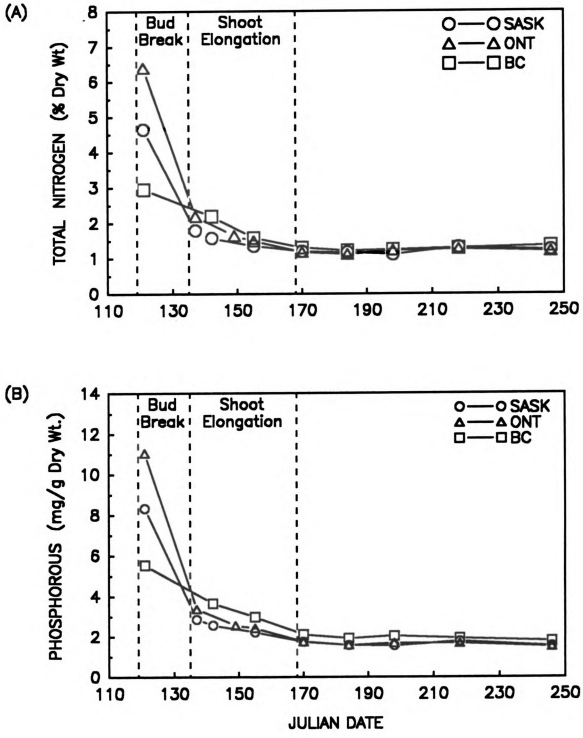

Figure 16. Seasonal variation of (A) total nitrogen and (B) phosphorous in current-year foliage of three seed sources in 1985.

tree for BC source), however these higher levels of nitrogen and phosphorous in the swelling vegetative buds agree with seasonal patterns generally observed in plant foliage (Mattson et al. 1983, Mattson and Scriber 1987).

The levels of potassium in ONT and BC trees decreased from averages of 17-18 mg/g (dw) in mid-May to less than 10 mg/g by mid-July (Figure 17A). In contrast, potassium levels in SASK trees increased during shoot elongation from 12.6 to 15.5 mg/g, and then decreased to levels during the rest of the summer that were significantly lower ($P \leq 0.05$) than those of BC trees (Table 14).

Levels of calcium, magnesium, copper and zinc in current-year foliage decreased and then increased over the course of the spring and summer (Figures 17B, 18A, 19A, 20B). The decreases occurred during shoot elongation. The increase in calcium began in early June at the end of the shoot elongation period, and by September reached levels 60% to 90% higher than those of mid-May. Increases in magnesium, copper and zinc occurred later in the summer and yielded end-of-season levels not substantially different from those of mid-May.

Trends in the levels of manganese, iron and sodium are less clear, although the levels of manganese and iron generally increased during the summer (Figures 18B, 19B, 20A). SASK trees had significantly ($P \leq 0.05$) lower levels of manganese than were found in BC trees and significantly higher levels of iron than were found in ONT trees (Table 14).

Water Content and Leaf Toughness -- Water content of the current-year foliage in 1986 peaked at ca. 80%, soon after budbreak in mid-May and then steadily decreased during the shoot growth period to less than 60% by mid-July (Figure 21A). The patterns of variation in water content were very similar among seed sources, however, the peak and decline of water content in the early-flushing SASK seed source were about one to two weeks advanced over that of the other two seed sources.

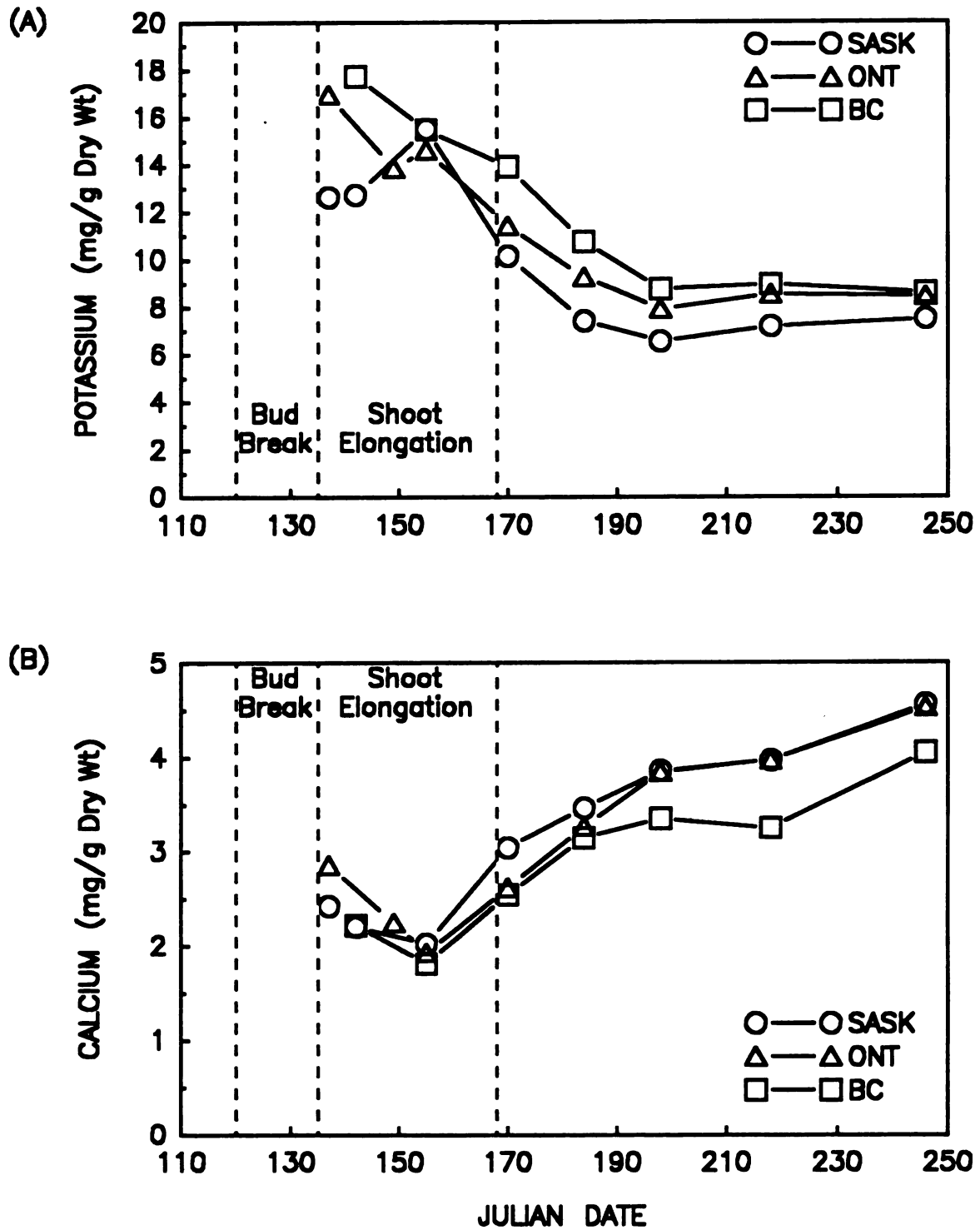

Figure 17. Seasonal variation of (A) potassium and (B) calcium in current-year foliage of three seed sources in 1985.

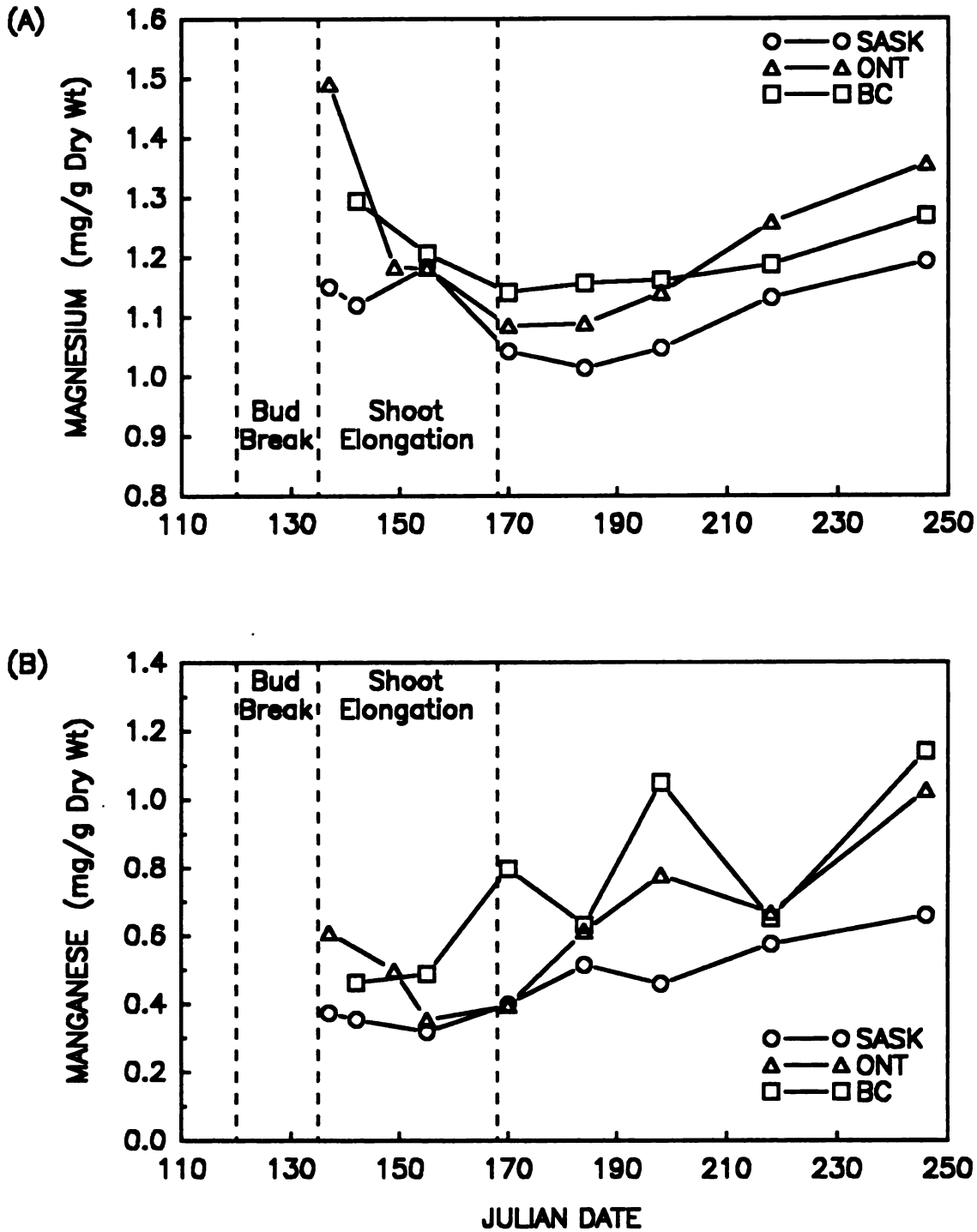

Figure 18. Seasonal variation of (A) magnesium and (B) manganese in current-year foliage of three seed sources in 1985.

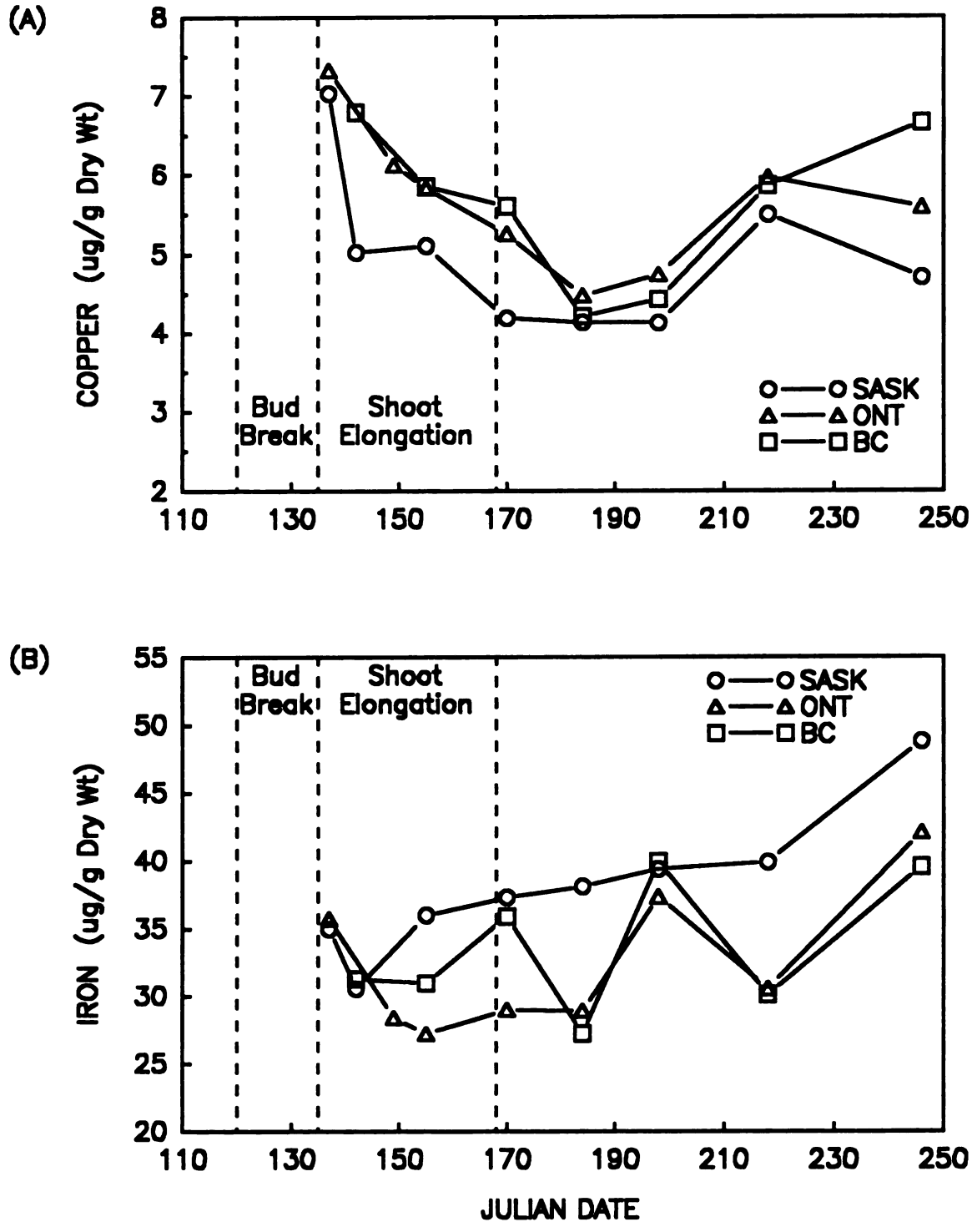

Figure 19. Seasonal variation of (A) copper and (B) iron in current-year foliage of three seed sources in 1985.

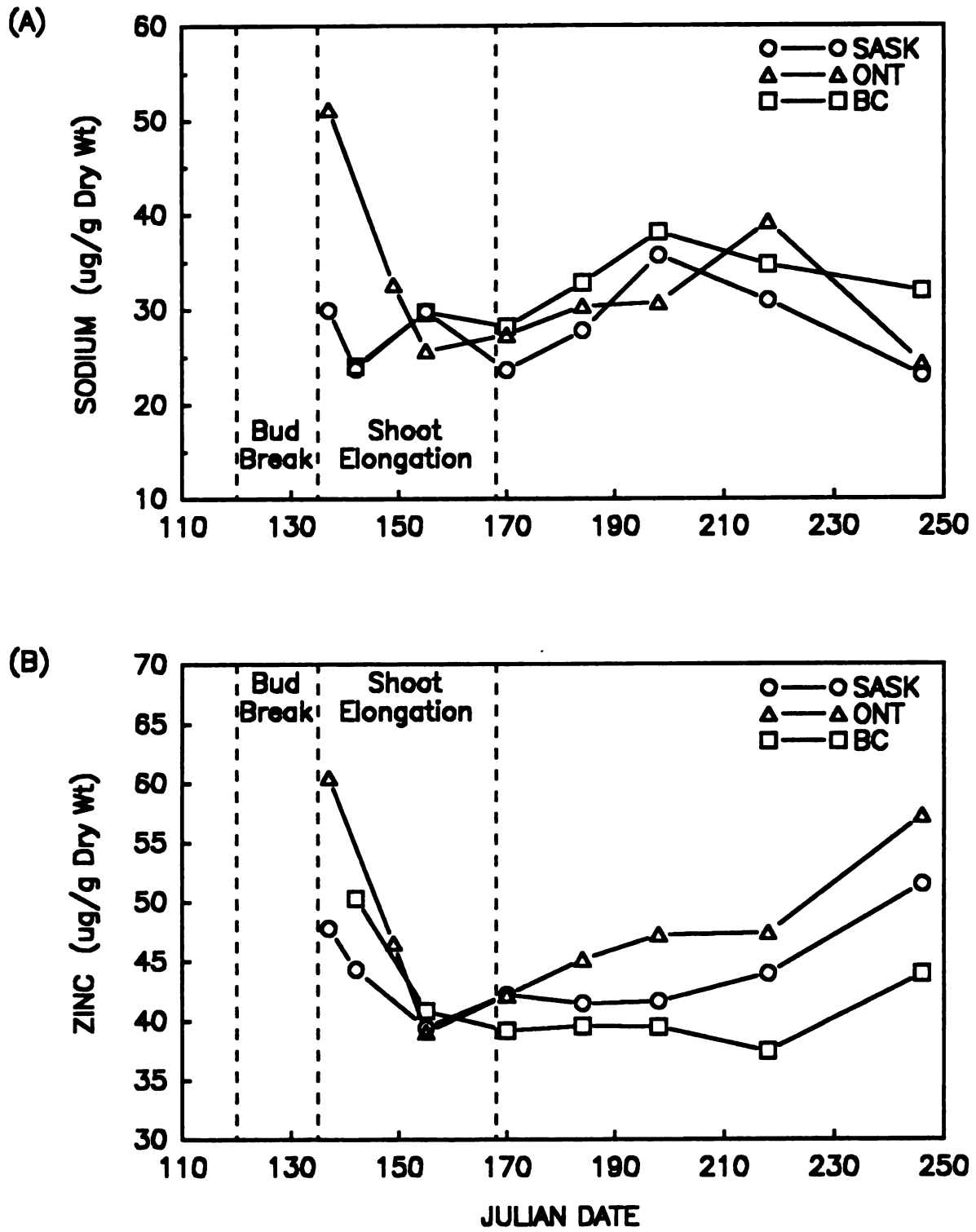

Figure 20. Seasonal variation of (A) sodium and (B) zinc in current-year foliage of three seed sources in 1985.

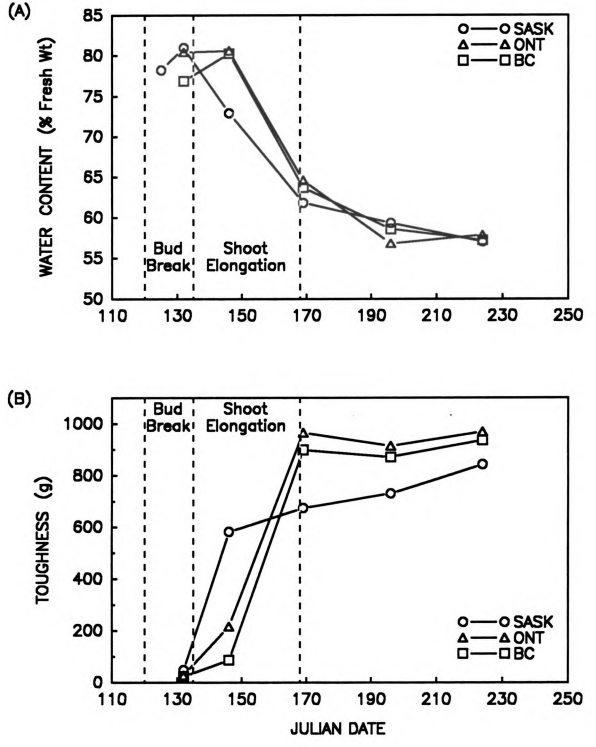

Figure 21. Seasonal variation of (A) water and (B) toughness in current-year foliage of three seed sources in 1986.

Toughness of the new leaves, on the other hand, increased rapidly during the period of shoot elongation (Figure 21B). The more advanced phenology of the SASK seed source was again indicated by an earlier increase in toughness. However, the pattern of increasing toughness in SASK trees differed from that of the other two seed sources. Toughness increased rapidly in SASK leaves up to 582 g in late May (JD 146), when new shoots were 90% elongated. Leaf toughness continued to increase but at a slower rate throughout the summer until reaching a peak of 843 g in mid-August (JD 224). In contrast, leaves on ONT and BC trees increased in toughness only during the period of shoot elongation (early June). However, leaf toughness at the end of this period on these seed sources peaked at higher values (965 g and 899 g, respectively) than occurred a full two months later on SASK trees.

One-Year-Old Foliage

One-year-old foliage was sampled from all trees at less than one week prior to budbreak on the earliest-flushing trees (equivalent to one to two weeks prior to budbreak on late-flushing trees). These samples were analyzed as was current-year foliage for nitrogen, nine minerals, water and toughness (Table 15). The levels of many of these foliar traits were similar to the levels observed in current-year foliage at the end of the summer (Figures 16-21). However, water was one of the major exceptions to this trend. Water content of old foliage was ca. 46%, about one-fifth less than the mid-August level of 57% in new foliage.

Relationship of Host Susceptibility to Host Phenology

The relationships between budworm performance and host quality were examined in two ways using host foliar values occurring during early larval

Table 15. Mean values (±SE) of 12 foliar characteristics of one-year-old foliage on three white spruce seed sources sampled less than one week prior to budbreak on the earliest-flushing seed source.

Foliar Trait[1]	Units	N per Mean	< 1 Week Prior to Budbreak	1-2 Weeks Prior to Budbreak	
			SASK	ONT	BC
Nitrogen	% dw	3	1.12 (± 0.04)	1.21 (± 0.08)	1.22 (± 0.02)
Phosphorous	mg/g dw	3	1.46 (± 0.07)	1.45 (± 0.12)	1.49 (± 0.09)
Potassium	mg/g dw	3	6.97 (± 0.79)	6.80 (± 0.61)	6.70 (± 0.69)
Calcium	mg/g dw	3	5.24 (± 0.96)	5.77 (± 0.41)	4.61 (± 0.73)
Magnesium	mg/g dw	3	1.09 (± 0.06)	1.19 (± 0.03)	1.15 (± 0.01)
Manganese	mg/g dw	3	1.01 (± 0.29)	1.36 (± 0.22)	1.44 (± 0.21)
Copper	μg/g dw	3	3.51 (± 0.16)	4.53 (± 0.44)	4.11 (± 0.14)
Iron	μg/g dw	3	55.2 (± 11.2)	47.2 (± 11.6)	39.0 (± 0.73)
Sodium	μg/g dw	3	22.4 (± 0.7)	22.0 (± 2.4)	28.6 (± 3.2)
Zinc	μg/g dw	3	60.5 (± 10.0)	68.0 (± 7.6)	54.6 (± 5.2)
Water Content	% fw	8	46.0 (± 0.005)	46.5 (± 0.002)	45.7 (± 0.003)
Toughness	g	80	859.4 (± 12.2)	965.5 (± 6.2)	890.5 (± 9.6)

[1] Nitrogen and minerals sampled on 1 May 1985. Water content and toughness sampled on 28 April 1986.

development and those during late larval development. All data used in these analyses except foliar levels of water and toughness were collected in 1985. Values of water and toughness were determined for each observation in the data set by interpolation of water and toughness data from 1986 using the appropriate elapsed degree day values for early and late larval development.

Canonical Correlation Analyses

Budworm performance and host quality data were first analyzed using canonical correlation techniques. The relationships revealed by these analyses are similar for foliar traits during both early and late larval development, although the relative importance of some variables differed (Table 16).

Four pairs of canonical variates (linear combinations of original variables) were produced for each of the two analyses (early foliar traits and late foliar traits). Each pair of canonical variates consists of an insect performance variate and a host quality variate. However, biologically meaningful relationships were demonstrated in only the first pair of canonical variates in each analysis. Lack of meaningful relationships in the second, third and fourth pairs of canonical variates was indicated by low loadings (absolute values < 0.50) for almost all variables and by low levels of redundancy. Redundancy is a measure of the proportion of variance in one set of original variables (here, insect performance) that is explained by the canonical variate of the other data set (host quality) (Smith 1981). The redundancy estimates for the first pair of canonical variates were 69.4% in the early foliar trait analysis and 76.1% in the late foliar trait analysis. Redundancy was 3% or less for each of the other three pairs of canonical variates in each of the two analyses. The canonical correlation between the insect performance variate and the host quality variate was 0.95 for the first canonical variate in both the early and the late foliar trait analyses.

Table 16. Canonical correlation analysis of insect performance and host quality using host foliar values during early larval development and late larval development.

Variables	Correlation of Original Variable With First Canonical Variate	
	Early Larval Development (Cohorts 3-8)	Late Larval Development (Cohorts 1-8)
Insect Performance:		
Larval Survival	0.877	0.909
Length of Development[1]	-0.905	-0.920
Adult Dry Weight	0.779	0.882
Growth Rate	0.932	0.959
Host Quality:		
Total Sugar	0.622	0.588
Nitrogen	0.964	0.692
Phosphorous	0.919	0.737
Potassium	0.679	0.788
Calcium	-0.309	-0.736
Magnesium	0.541	0.138
Manganese	-0.195	-0.558
Copper	0.478	0.241
Iron	0.092	-0.347
Sodium	0.255	-0.136
Zinc	0.628	-0.033
Water Content[2]	0.858	0.984
Toughness[2]	-0.900	-0.854

Table 16 (cont'd.)

	Early Larval Development (Cohorts 3-8)	Late Larval Development (Cohorts 1-8)
Canonical Correlation	0.952	0.950
Redundancy[3]	0.694	0.761

[1] Length of development measured in degree days.

[2] Water content and toughness data collected in 1986. All other data collected in 1985.

[3] Proportion of variance in original insect performance variables explained by host quality canonical variate.

The patterns of loadings for insect performance variables in the first canonical variate were consistent between the early foliar trait analysis and the late foliar trait analysis. Larval survival, adult dry weight and growth rate were positively correlated, whereas length of development was negatively correlated with the first canonical variate. All correlations of insect performance with the first canonical variate had absolute values of greater than 0.77 in each analysis. Thus, the first canonical variate for these four variables provides a strong linear representation of insect performance.

In the analysis of foliar traits during early larval development, the host quality variables that had the highest loadings (absolute values greater than 0.85) were nitrogen, phosphorous, water content and toughness. Nitrogen, phosphorous and water content were positively correlated whereas toughness was negatively correlated with the first canonical variate. A second grouping of host quality variables includes total sugar, potassium and zinc with positive loadings of 0.62, 0.68 and 0.63, respectively. A weak positive relationship is also indicated for magnesium with a loading of 0.54.

In the analysis of foliar traits during late larval development, water content and toughness again had high loadings (0.98 and -0.85) in the first canonical variate. However, nitrogen and phosphorous with loadings of 0.69 and 0.74 were less strongly correlated with the first canonical variate than in early larval development. Potassium had a high positive correlation of 0.79, and calcium had a high negative correlation of -0.74. Weak relationships were indicated for total sugar and manganese with loadings of 0.59 and -0.56, respectively.

The results of the canonical correlation analyses indicate that insect performance was positively correlated with foliar levels of water, nitrogen, phosphorous, potassium and total sugar and negatively correlated with leaf toughness during both periods of early and late larval development. There also

were positive relationships between insect performance and magnesium and zinc levels during periods of early larval development, and negative relationships between insect performance and calcium and manganese levels during late larval development. Insect performance did not appear to be related to levels of copper, iron or sodium.

Bivariate plots of data used in canonical correlation analysis were examined to evaluate the data for non-linear relationships that might affect the level of correlation. Insect performance had slightly non-linear relationships with water content and toughness during early larval development and with calcium during late larval development. However, all of these relationships approximated linearity, and these host quality variables had high loadings on the first canonical variate.

Ordination of Canonical Scores

An ordination technique using two-dimensional plots of canonical scores (Smith 1981) provides a useful way to compare insect performance and host quality relationships among seed sources and budworm cohorts. Separate plots were prepared for each seed source using canonical scores from the canonical correlation analysis of late larval development (Figures 22-24). Each point on a plot represents one cohort on one tree (number indicates cohort). Three groups of cohorts are indicated on each plot: cohorts 1 to 3 were started at weekly intervals from 23 April to 7 May; cohorts 4 to 6 were started at weekly intervals from 14 May to 28 May; and cohorts 7 and 8 at monthly intervals on 25 June and 23 July.

The ordination technique clearly illustrates the positive relationship between host nutritional quality and insect performance. Host quality and insect performance both decrease with progressively later budworm cohorts. These

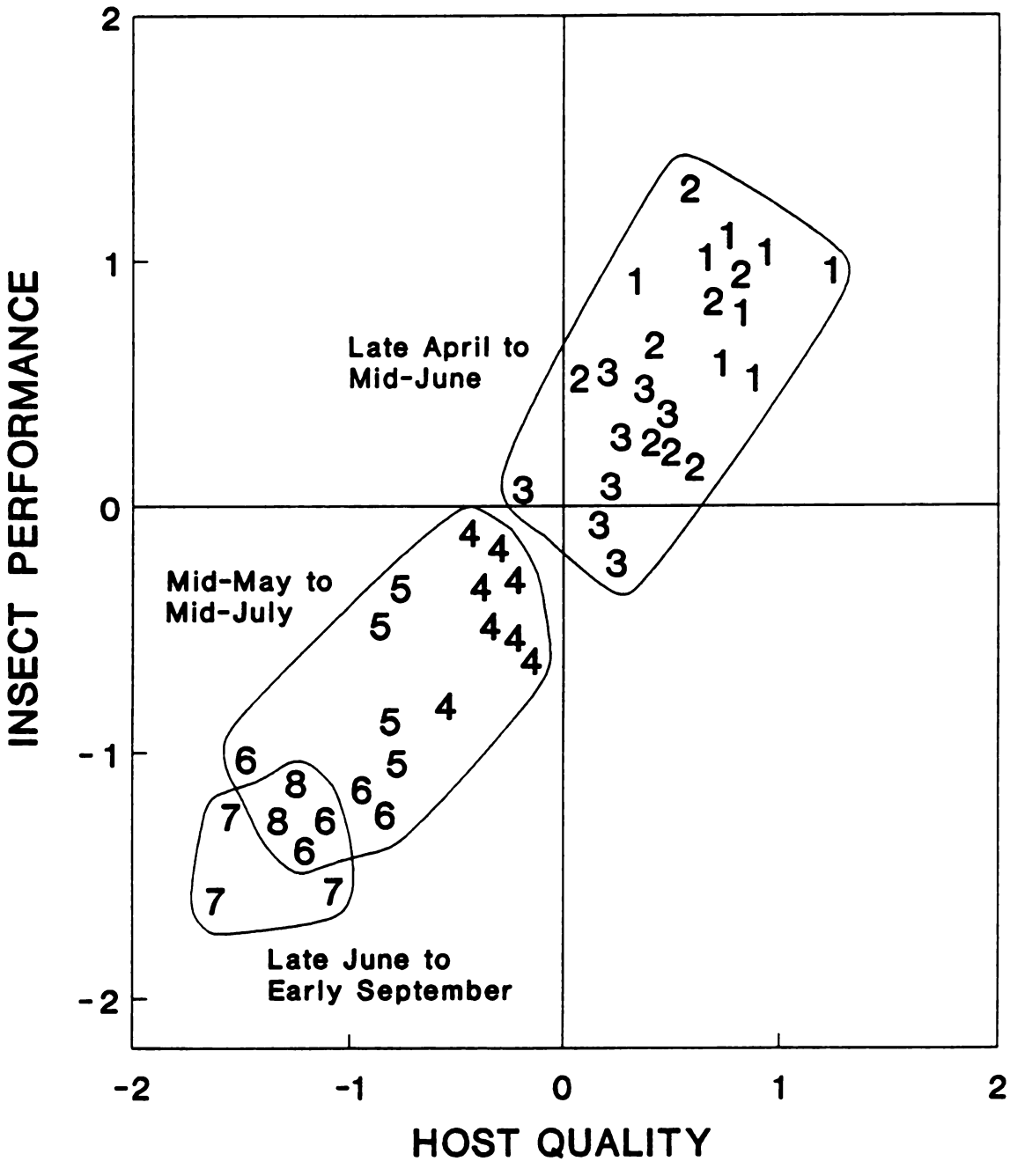

Figure 22. Ordination of canonical scores for insect performance and host quality during late larval development on the SASK seed source. Numbers within graph indicate cohorts on individual trees.

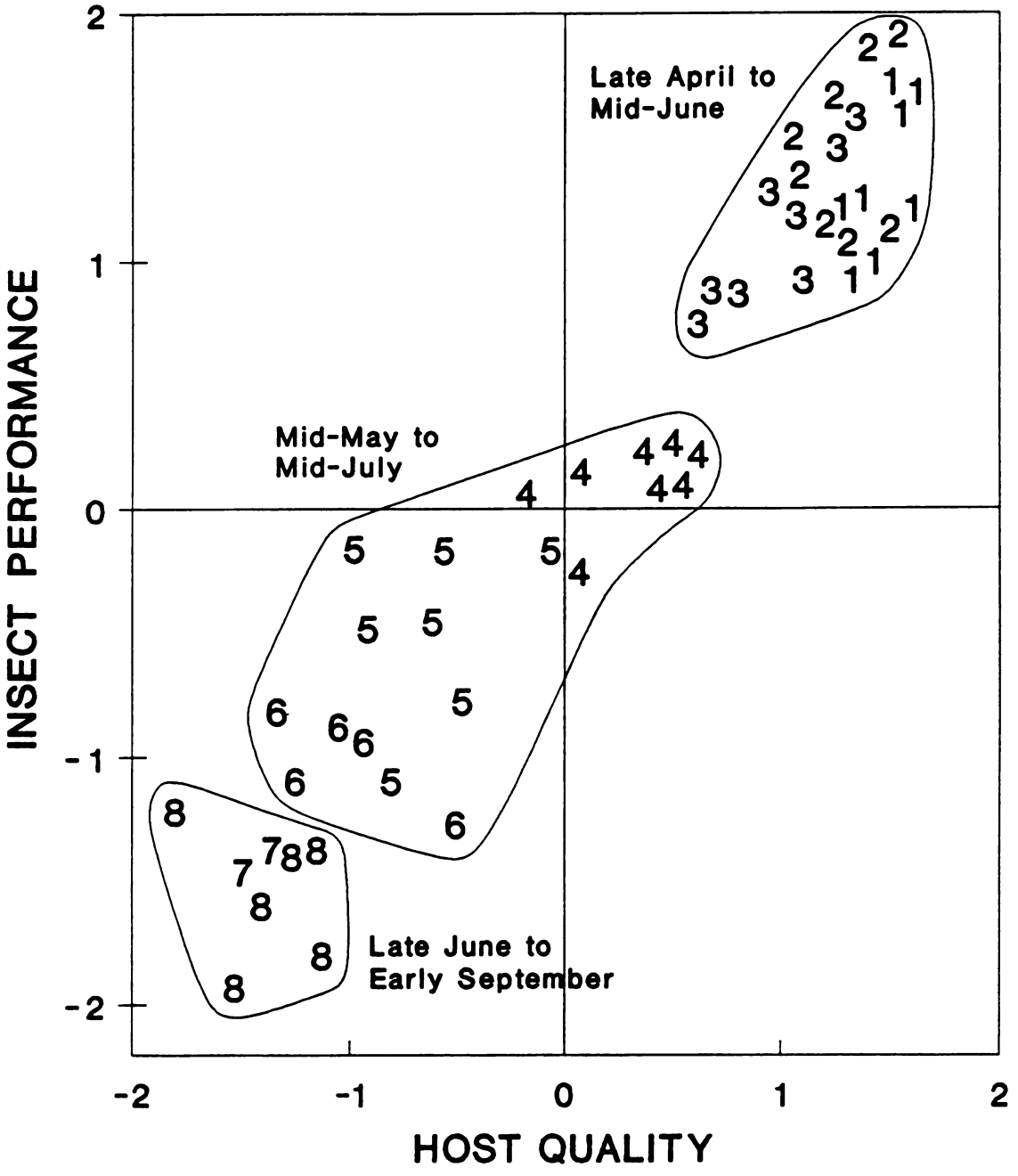

Figure 23. Ordination of canonical scores for insect performance and host quality during late larval development on the ONT seed source. Numbers within graph indicate cohorts on individual trees.

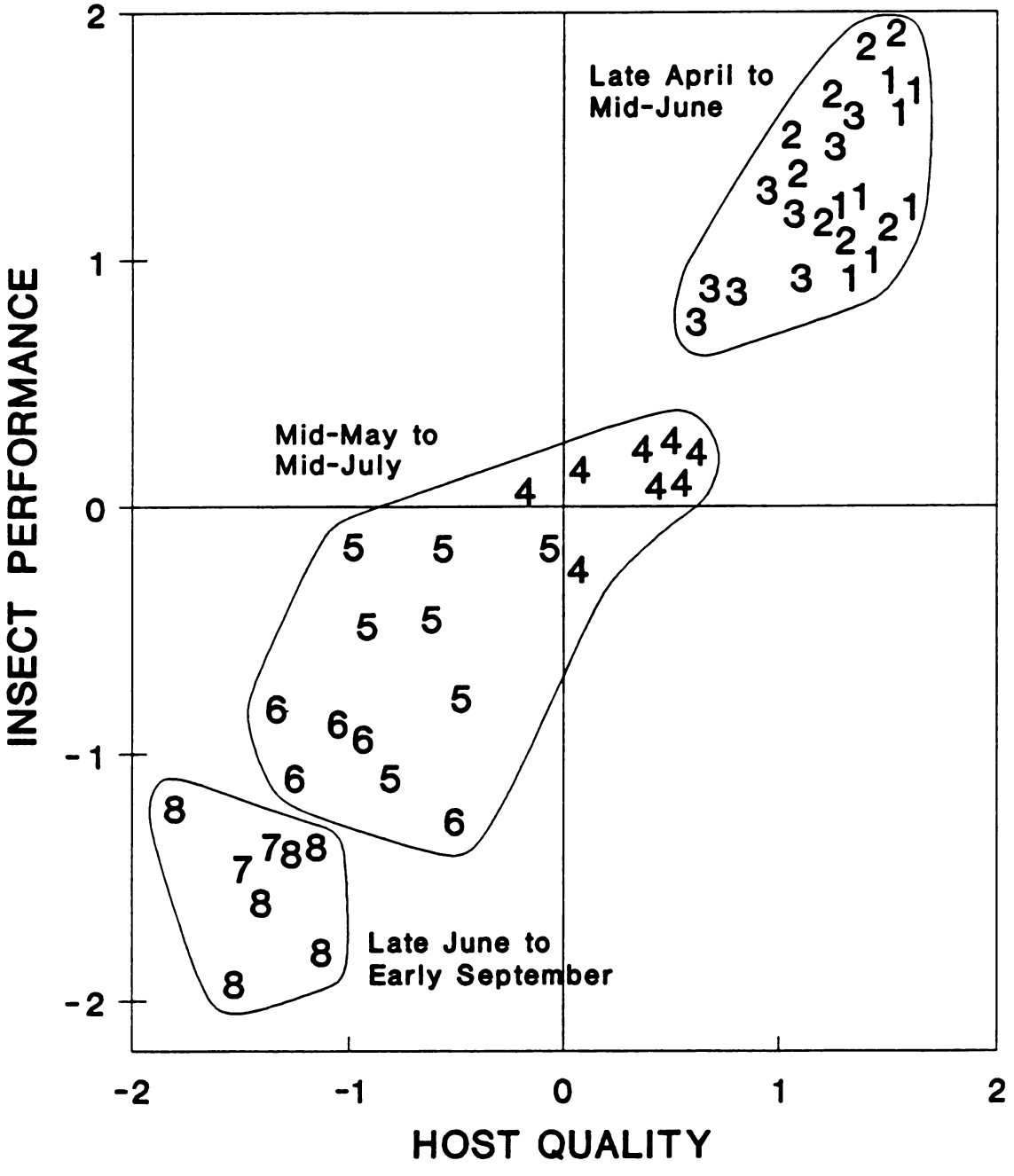

Figure 23. Ordination of canonical scores for insect performance and host quality during late larval development on the ONT seed source. Numbers within graph indicate cohorts on individual trees.

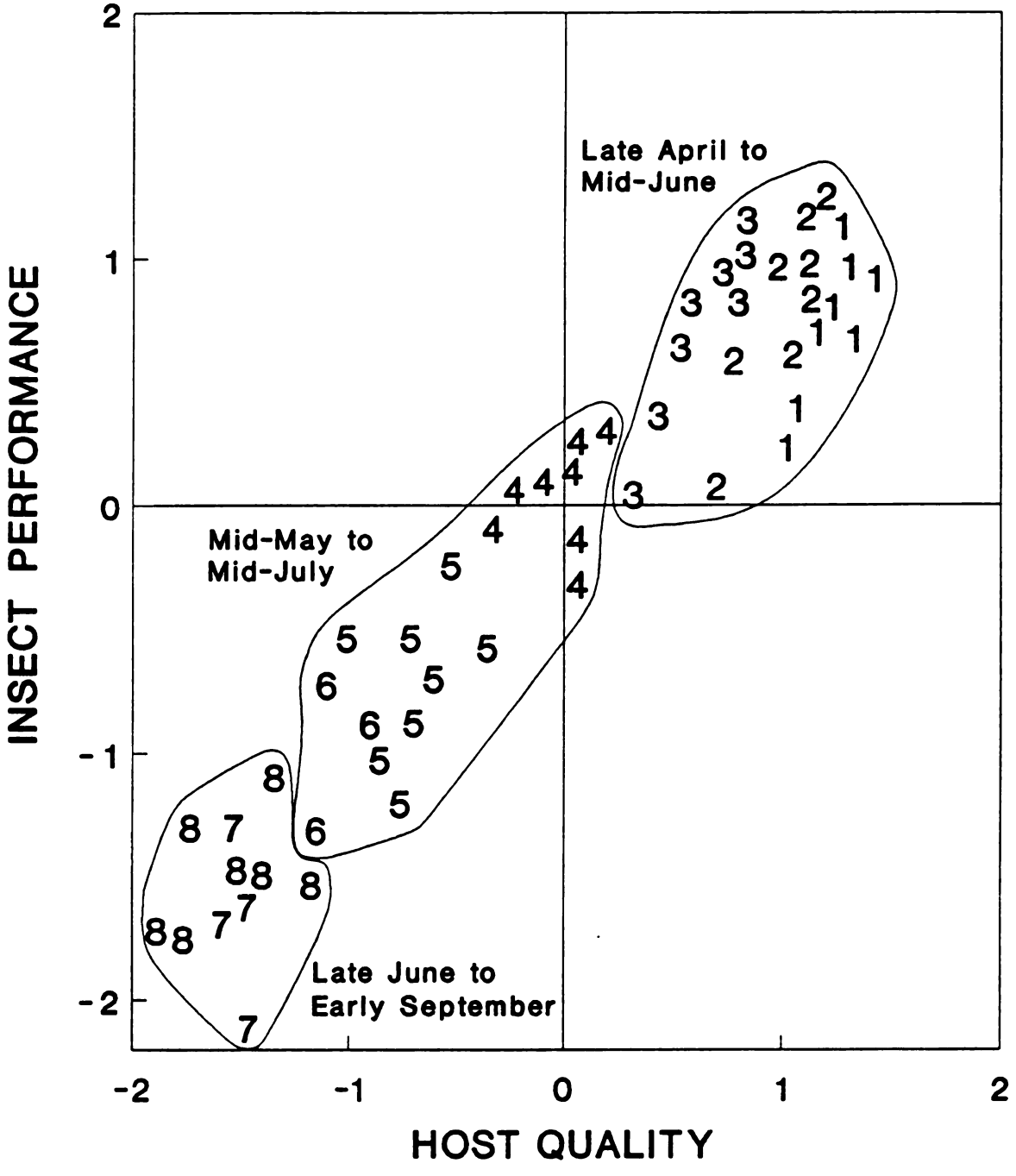

Figure 24. Ordination of canonical scores for insect performance and host quality during late larval development on the BC seed source. Numbers within graph indicate cohorts on individual trees.

changes occur quickly during the spring (cohorts 1 to 6), but only slight changes occur during the summer (cohorts 6 to 8). Seed source differences can also be seen among the plots. Cohorts 1 to 3 had the best host quality and performed the best on the ONT seed source (Figure 23). Comparison of the locations of cohorts 1 to 4 on the three plots reveals the effects of the earlier phenology of the SASK seed source. These points on the SASK plot are shifted more to the lower left than on the ONT and BC plots. Among ONT and BC trees, insect performance in cohorts 1 to 3 changed only slightly while host quality was decreasing.

Regression Analyses

Regression analysis of budworm performance and host quality was performed using larval survival and individual foliar traits. Bivariate plots of budworm performance data with foliar trait data revealed that the relationships of larval survival, adult weight and budworm growth rate with individual foliar variables were nearly identical. The relationships of length of development with foliar variables were, as expected, opposite to that of the other three budworm performance variables. Therefore, larval survival is presented here as an overall indicator of budworm performance in regression analysis.

The results of regression analysis support the conclusions of the canonical correlation analyses. The strongest relationships between survival and foliar variables were with levels of nitrogen, phosphorous, water and toughness during early larval development and levels of phosphorous, potassium, calcium, water, and toughness during late larval development. These results were obtained using the same data set used in the canonical correlation analyses. However, some additional data, that were not included in canonical correlation analyses because of the requirement of a balanced data set, were available for regression analysis. These data included observations from branches that had 0% larval survival in

some later cohorts and data for nitrogen, phosphorous, water and toughness during early development in cohorts 1 and 2. The following discussion of individual foliar variables is based on regression analyses of data sets including these additional observations.

Larval survival was positively associated with foliar levels of total sugar, nitrogen, phosphorous, potassium and water and negatively associated with foliar levels of calcium and toughness (Figures 25-31). The general trends of these relationships were the same for foliar levels during early larval development and during late larval development. However, in several cases the strength of association or the pattern (linear vs. non-linear) of the relationships did vary between early and late development. All regression equations illustrated in Figures 25-31 are significant ($P < 0.01$). As indicated by canonical analysis, the positive relationship between larval survival and total sugar (Figure 25) was relatively weak ($r^2 < 0.40$). This relationship was similar for foliar levels of sugar during both early larval development and during late larval development.

The relationships of larval survival with levels of nitrogen and phosphorous were very similar (Figures 26 and 27). Foliar levels of nitrogen and phosphorous varied much more during early larval development than during late larval development. Nitrogen had a range of 1% to 6% and phosphorous had a range of 1 to 10 mg/g during early larval development. Larval survival was positively associated with nitrogen, up to nitrogen levels of about 2.5% to 3%. Thereafter, survival appeared to level off or possibly decline, although there were few observations in this category. A similar non-linear relationship existed between larval survival and the level of phosphorous during early larval development. Larval survival was greatest at phosphorous levels of at least 4 to 5 mg/g. The levels of nitrogen and phosphorous during late larval development varied over much smaller ranges. Nevertheless, regression analysis revealed highly significant

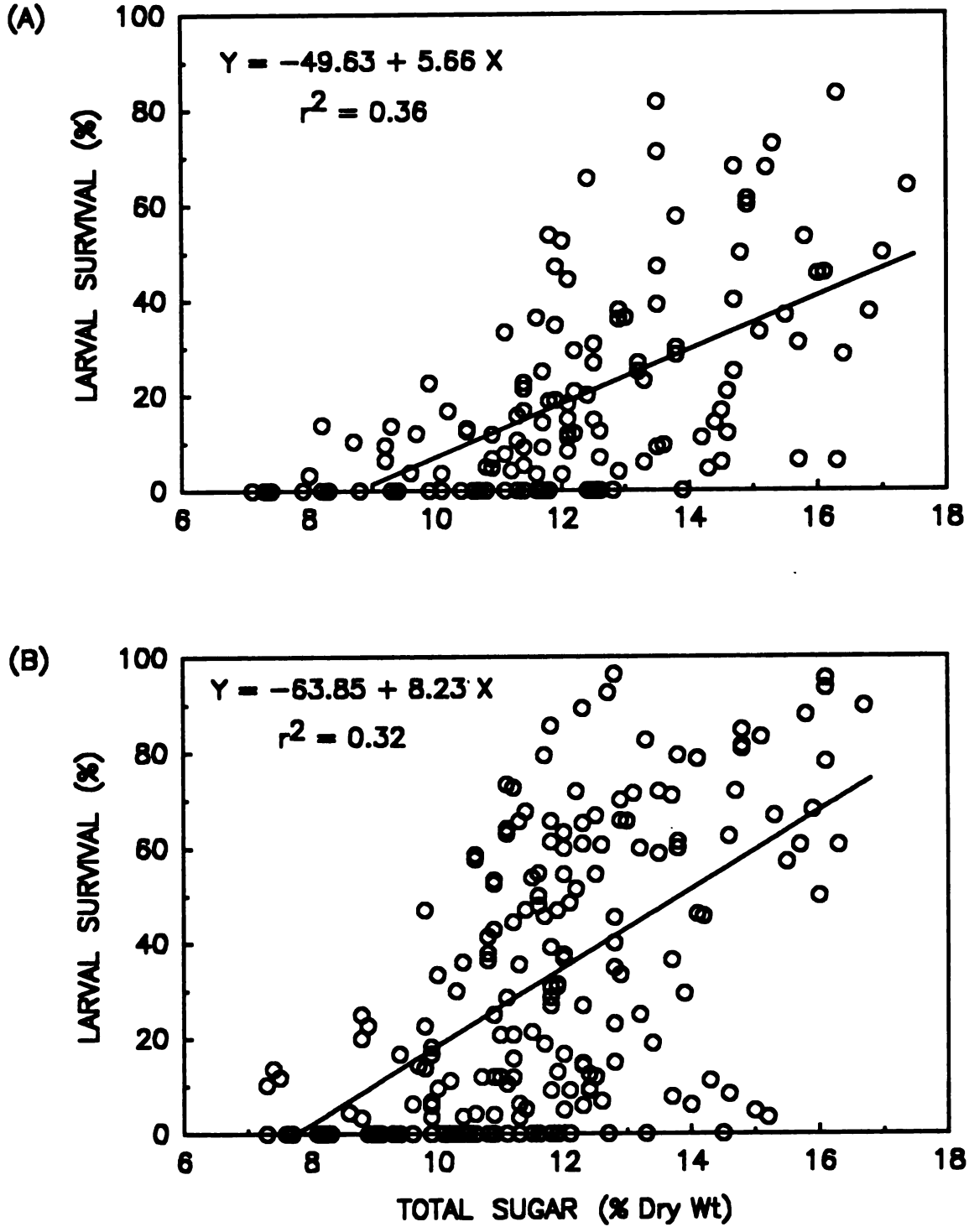

Figure 25. Relationship of percent larval survival and total sugar in current-year foliage during (A) early larval development and (B) late larval development.

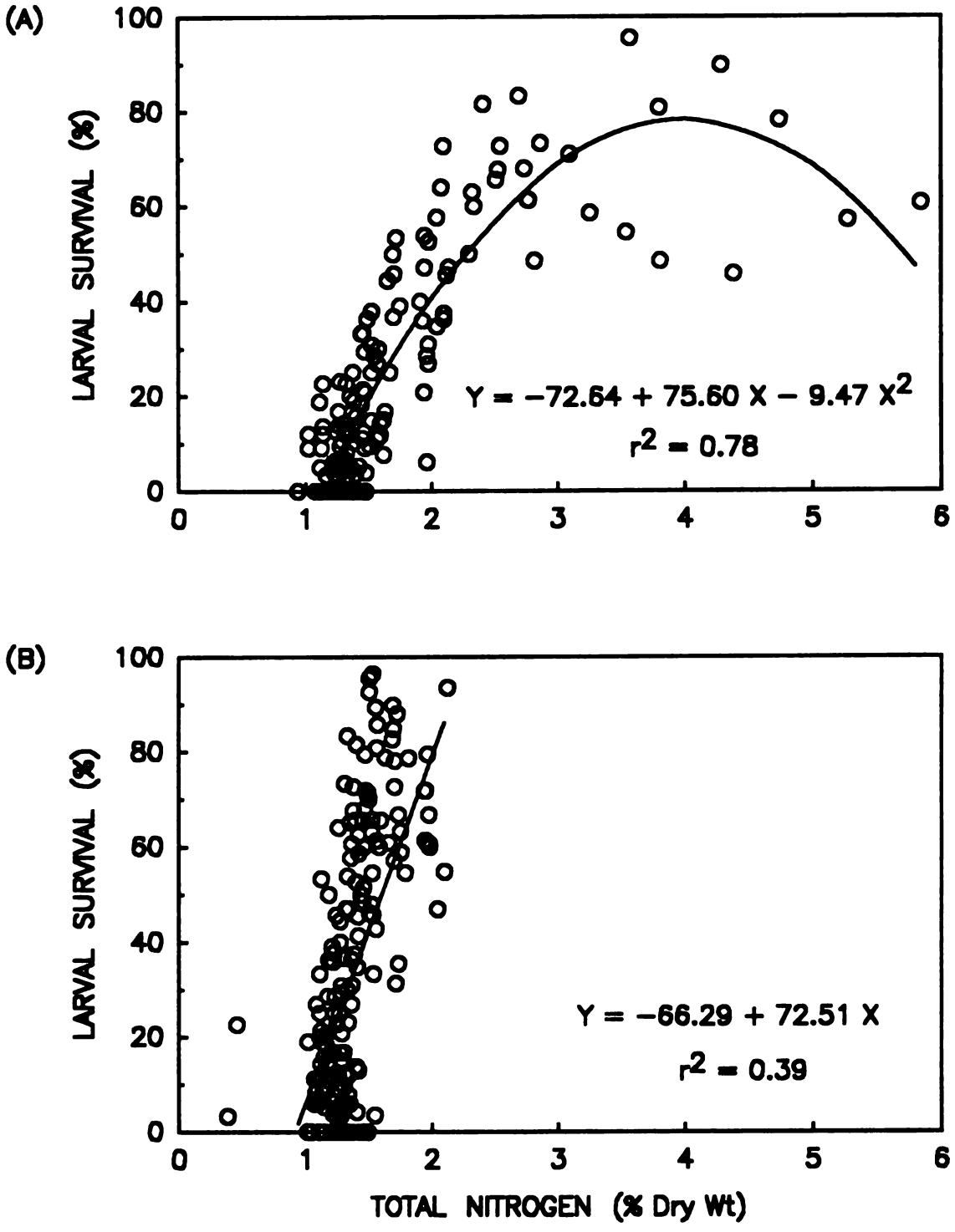

Figure 26. Relationship of percent larval survival and total nitrogen in current-year foliage during (A) early larval development and (B) late larval development.

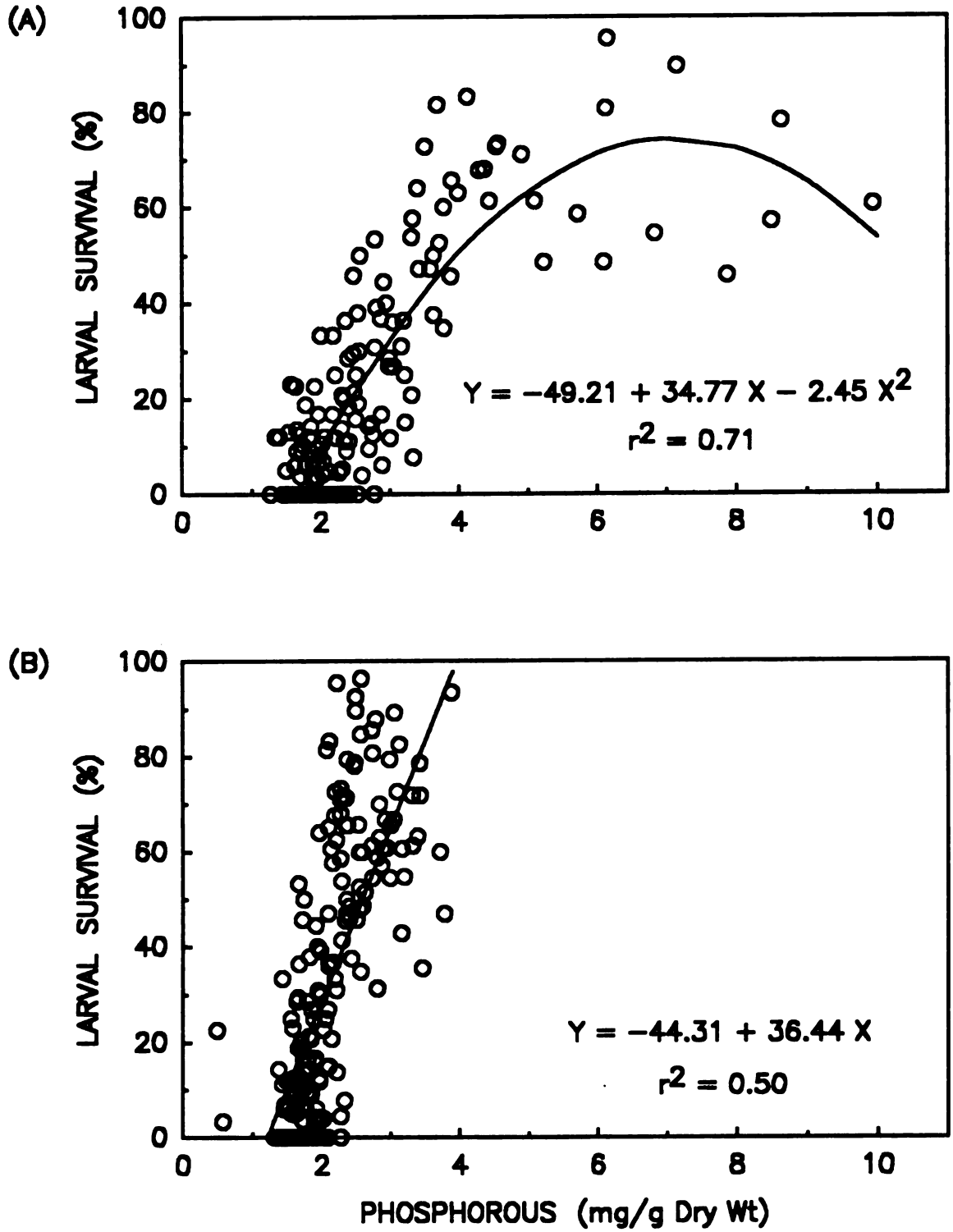

Figure 27. Relationship of percent larval survival and phosphorous in current-year foliage during (A) early larval development and (B) late larval development.

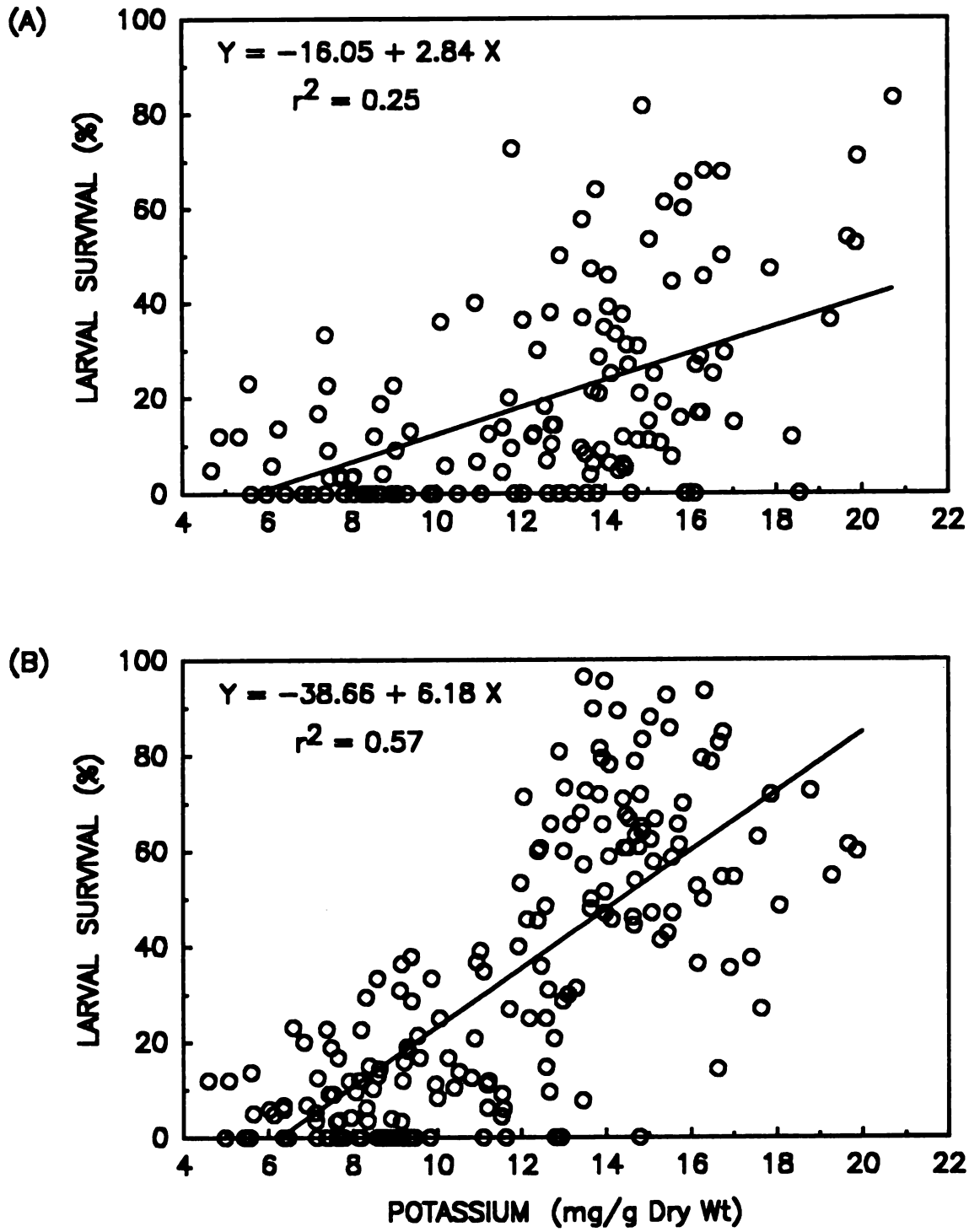

Figure 28. Relationship of percent larval survival and potassium in current-year foliage during (A) early larval development and (B) late larval development.

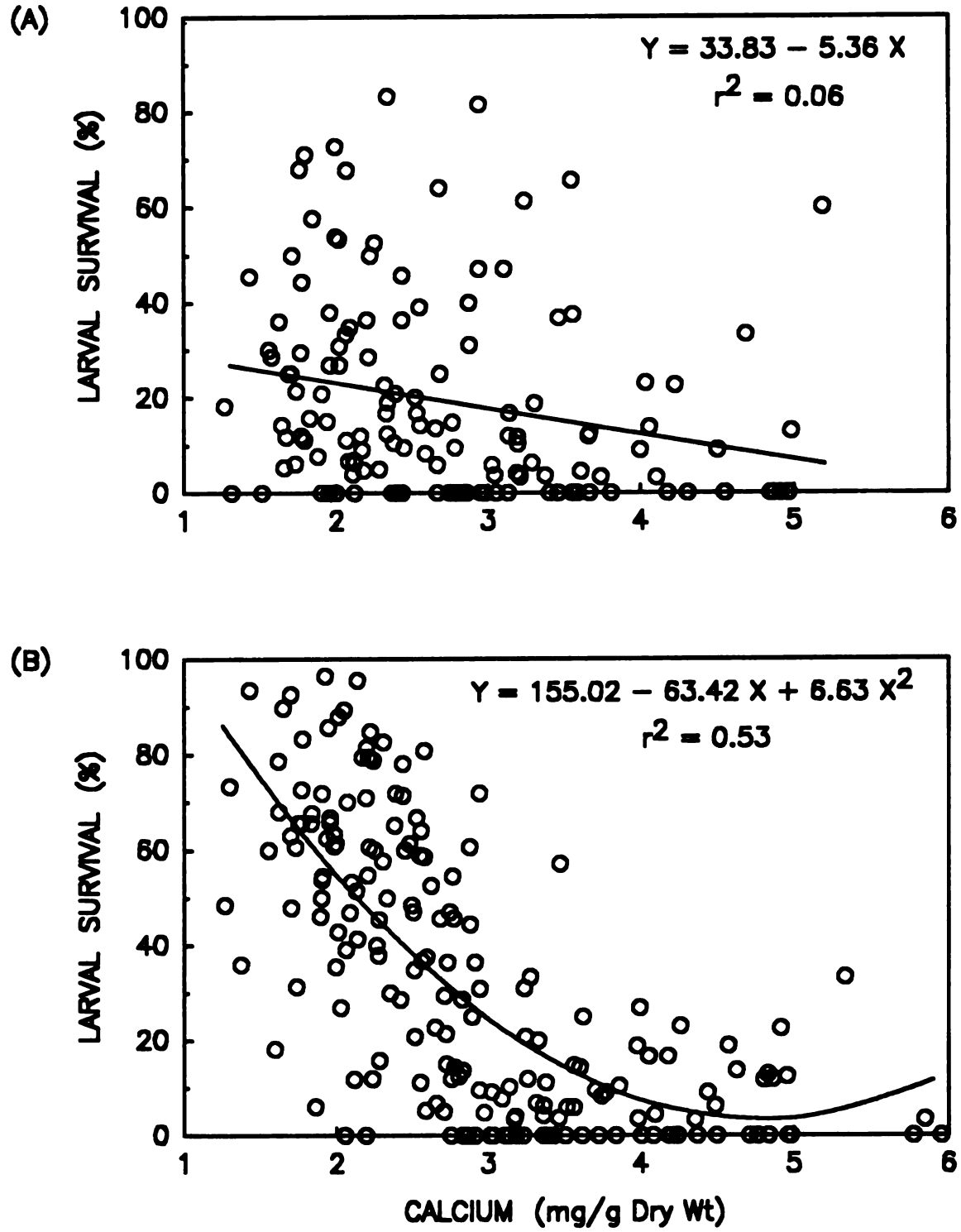

Figure 29. Relationship of percent larval survival and calcium in current-year foliage during (A) early larval development and (B) late larval development.

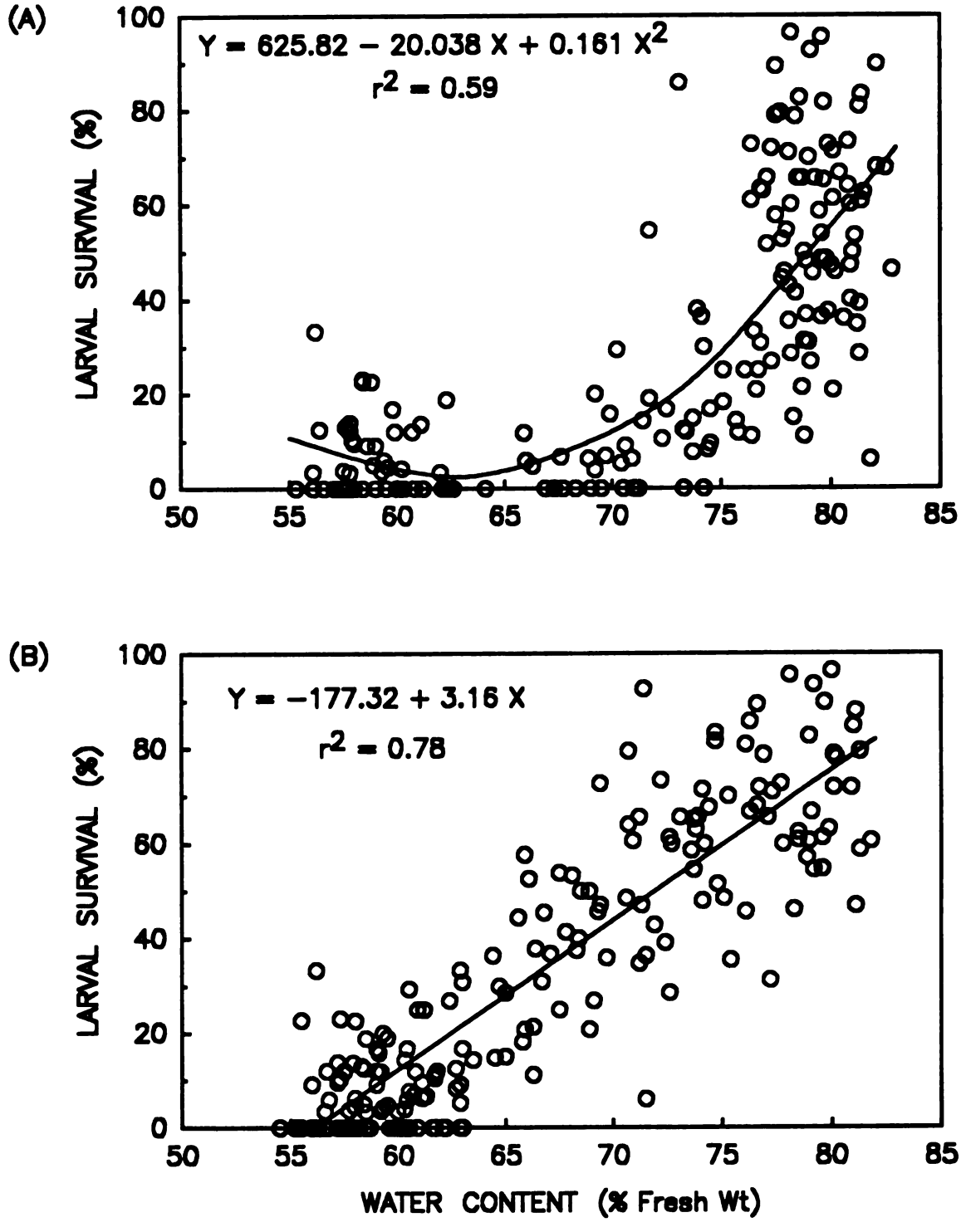

Figure 30. Relationship of percent larval survival and water content in current-year foliage during (A) early larval development and (B) late larval development.

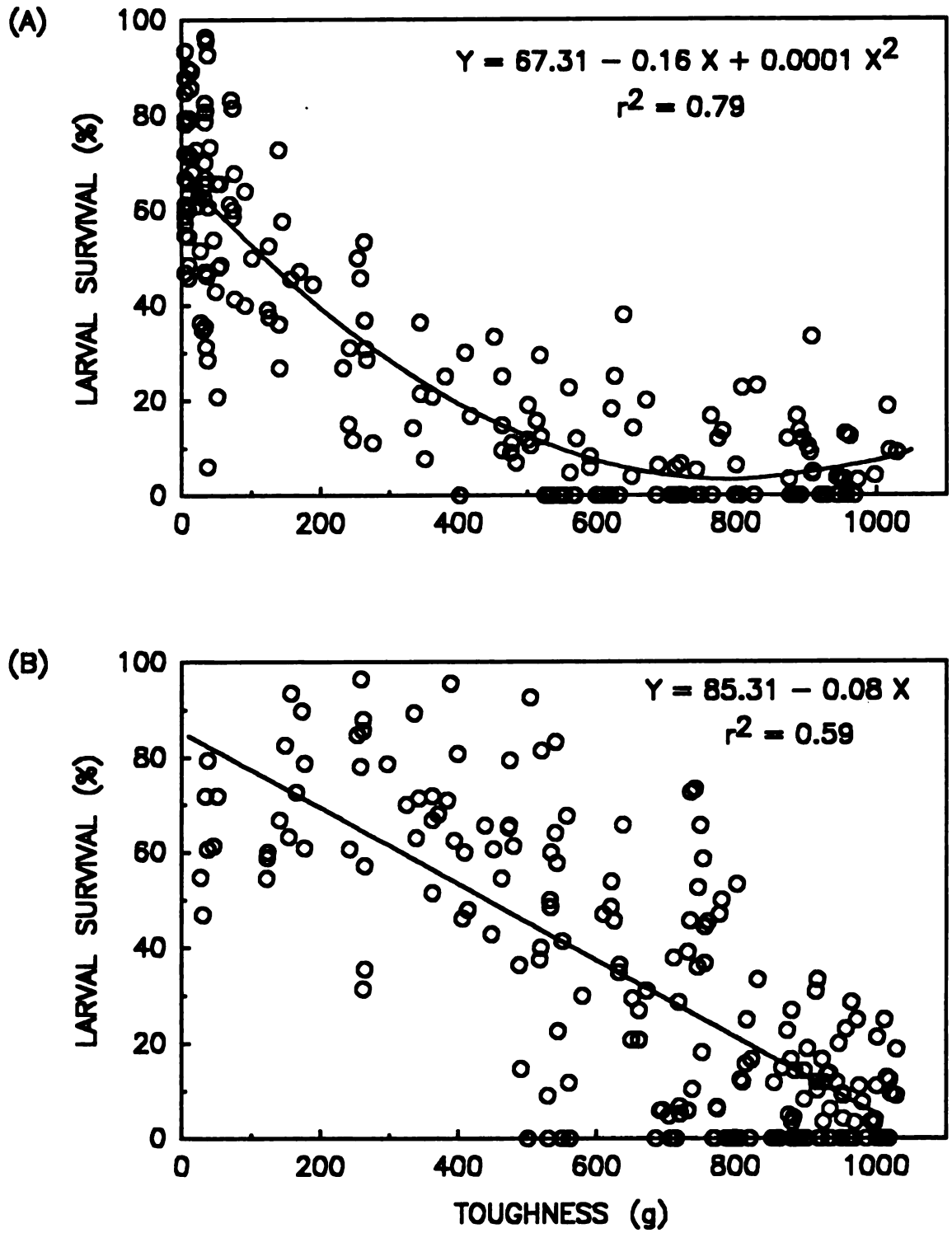

Figure 31. Relationship of percent larval survival and toughness of current-year foliage during (A) early larval development and (B) late larval development.

relationships ($P < 0.0001$) between larval survival and the foliar levels of these nutrients during late larval development.

Larval survival was also positively associated with the levels of potassium but negatively associated with the levels of calcium during late larval development (Figures 28 and 29). A weak relationship also existed between survival and potassium levels during early larval development.

The relationships of larval survival with foliar levels of water and toughness were non-linear for foliar levels during early larval development and linear for levels during late larval development (Figures 30 and 31). Larval survival was low (< 40%), when water content was < 75% and toughness was > 300 g during early larval development.

Among the other foliar nutrients measured, regression analyses revealed minor relationships ($r^2 < 0.25$) between larval survival and foliar levels of magnesium, manganese and zinc. Survival was positively associated with magnesium and zinc levels during early larval development and negatively associated with manganese levels during late larval development.

Many models of relationships between budworm performance variables and two or more foliar variables were developed with multiple regression techniques. For each budworm performance variable (survival, weight, growth rate and length of development), there were always several significant ($P \leq 0.05$) models. It was difficult to select only a few models that best described the relationships of budworm performance with host quality. Three and four-variable models that explained a high proportion of the variation in budworm performance ($r^2 > 0.7$) frequently excluded some foliar variables that previous analyses (canonical correlation and individual regressions) had indicated were important. This multiplicity of highly significant models is due to a high level of intercorrelation among many of the foliar variables measured in this study (Tables 17 and 18).

Table 17. Pearson correlation coefficients[1] among 10 major foliar variables for foliar levels during early larval development (cohorts 3-8, N = 136).

	N	P	K	Ca	Mg	Mn	Zn	Water	Tough-ness
Total Sugar	.54	.53	.42	-.38	.22	-.17	.24	.68	-.62
N	--	.95	.62	-.27	.55	*	.56	.75	-.84
P	--	--	.72	-.39	.54	*	.49	.81	-.86
K	--	--	--	-.52	.49	-.27	.30	.78	-.72
Ca	--	--	--	--	.29	.50	.43	-.62	.46
Mg	--	--	--	--	--	.22	.74	.32	-.40
Mn	--	--	--	--	--	--	.19	-.39	.31
Zn	--	--	--	--	--	--	--	.27	-.37
Water	--	--	--	--	--	--	--	--	-.91

[1] All correlations, except those marked with an asterisk, are significant ($P \leq 0.05$).

Table 18. Pearson correlation coefficients[1] among 10 major foliar variables for foliar levels during late larval development (cohorts 1-8, N = 192).

	N	P	K	Ca	Mg	Mn	Zn	Water	Tough-ness
Total Sugar	.39	.38	.38	-.42	*	*	*	.58	-.46
N	--	.91	.64	-.40	.36	*	.21	.71	-.76
P	--	--	.76	-.54	.35	-.21	*	.79	-.79
K	--	--	--	-.57	.31	-.33	*	.80	-.70
Ca	--	--	--	--	.36	.51	.59	-.72	.55
Mg	--	--	--	--	--	.35	.65	*	-.19
Mn	--	--	--	--	--	--	.24	-.47	.40
Zn	--	--	--	--	--	--	--	*	*
Water	--	--	--	--	--	--	--	--	-.87

[1] All correlations, except those marked with an asterisk, are significant ($P \leq 0.05$).

Thus, several foliar variables may be good "predictors" of budworm performance, but the determination of which foliar variable(s) are biologically important to budworm performance will be best done using experimental diets (Harvey 1974, McLaughlin 1986, Clancy et al. 1988b, Mattson et al. 1990). Perhaps the canonical analyses provide the best representation of the relationship between budworm performance and foliar properties. These analyses incorporate, simultaneously, most of the variables that one would expect to be important in regulating the growth and development of folivores.

DISCUSSION

Defining the Window of Susceptibility

Although the concept of a "window of susceptibility" in plants to herbivores has been in the literature for years, and in the everyday parlance of entomologists and ecologists (Mattson et al. 1982), this study is the first to comprehensively test the hypothesis, and to furthermore offer substantive support for it. Owing to the rather widespread and casual use of the term, window of susceptibility, there seems to be no precise definition for it except as implied in Mattson et al. (1982), i.e. growth and survival of the herbivore outside of the putative "window" is ecologically negligible. In other words, very few insects are capable of surviving and reproducing if they initiate or terminate feeding outside of the boundaries of the putative window.

In the case of white spruce and the spruce budworm, the window for successful development begins shortly before budbreak and terminates near the end of the period of active shoot elongation. This means that to achieve ecologically meaningful growth and reproduction, budworms must begin and finish growing between these temporal limits of the window. For example, budworm larval survival, adult weights and growth rates were highest for the first three cohorts that started feeding prior to or during budbreak and ended feeding and larval development by the time that shoot elongation ended. Later cohorts were substantially less successful than the first three, owing to greatly diminished survival and growth.

The window of susceptibility in white spruce may begin as early as four weeks prior to budbreak. The earliest cohorts in 1985 and 1987 began three and four weeks, respectively, before budbreak and had good success as measured by all performance variables. However, the survival of the cohort starting four weeks ahead of budbreak was less than expected from those starting three weeks or less before budbreak. Outbreaks of western spruce budworm epidemics in British Columbia have been associated with years when larval emergence preceded budbreak by 17-18 days (Thomson et al. 1984). Synchrony of larval emergence and host budbreak is also important for many other species of tree-feeding defoliators (Embree 1965, von Schönborn 1966, Wickman 1976, Witter and Waisanen 1978, Leather 1986, Turgeon 1986, Du Merle 1988).

The end of the window of susceptibility is associated with the end of active shoot growth. Budworms placed on the trees at the time of budbreak, in most cases, did not complete larval development until shortly after the end of shoot elongation. These insects, which include cohort 3 on SASK trees and cohort 4 on ONT and BC trees, were developing at the later limits of the window of susceptibility. The largest decreases (38%-53%) in larval survival occurred between cohort 3 and cohort 4 in each seed source (Figure 7). Only seven days separated the starting time for development of these two cohorts in the field. These results indicate a rather abrupt end of the window of susceptibility. Shepherd (1985) similarly observed high survival when western spruce budworm larvae emerged prior to swelling of buds, but very low survival when larval emergence occurred nearer to the time of budbreak. Strong et al. (1984) cited several examples in which insect-host asynchrony of only one or two weeks caused greatly reduced performance in insect herbivores. Thus, the phenological window can be interpreted as a race between the herbivore and the host plant. The insect

feeds on a plant that is rapidly deteriorating in food quality owing to nutrient dilution and buildup of tissue fiber content, and perhaps defenses too.

The beginning of the window of susceptibility in white spruce coincides well with the normal peak of spring emergence of overwintering larvae (ca. 100 accumulated degree days). However, budworm-tree asynchrony can occur with budworm phenology either too advanced or too retarded in relation to tree phenology (Blais 1957, Beckwith and Burnell 1982, Thomson et al. 1984, Raske 1985, Shepherd 1985). The cause of asynchrony may be related to differences in mechanisms controlling the emergence of larvae and the initiation of vegetative growth. Larval emergence is determined primarily by ambient air temperatures (Thomas 1976), although photoperiod also plays a role (Harvey 1958). On the other hand, initiation of vegetative growth is determined by soil temperatures as well as air temperatures (Cleary and Waring 1969, Lavender et al. 1973, Beckwith and Burnell 1982, Volney 1985).

Budworm-tree asynchrony was associated with the collapse of two western spruce budworm epidemics in British Columbia (Thomson et al. 1984). Asynchrony likewise occurred for three consecutive years (1981-83) during the collapse of the recent spruce budworm epidemic in Newfoundland (Raske 1985). In the latter case, larvae became active in the spring of each year at about two weeks after budbreak on balsam fir. This timing would be approximately equivalent to one week after budbreak on white spruce. Although parasitoids and diseases accounted for some larval mortality in these collapsing populations, many larvae died of unknown causes during the later instars.

Seed Source Effects

A seed source effect was present for all budworm performance variables except pupal survival (Table 3). In most cases budworm performance was lower on the early-flushing SASK seed source (Table 4). Is seed source effect related to different timing of phenology among the seed sources? Analyses of phenologically similar hosts (Tables 5 and 6) indicated that phenological differences among seed sources accounted for most of the seed source effect on two budworm performance variables: larval survival (Figure 7) and length of development in degree days (Figure 8). The effect is particularly evident for length of development. The shortest budworm development time (in degree days) occurred in cohort 1 on SASK trees, in cohort 2 on ONT trees and in cohorts 2 and 3 on BC trees (i.e. the same relative order of tree phenology). Thus, budworm development required the fewest degree days for those insects that began spring larval development at two weeks prior to budbreak. The seed source effect on other budworm performance variables (growth rate, adult weight and length of development in days), however, was apparently related to some factor other than, or in addition to, phenological differences.

The seed sources used in this study are from widely separated parts of the white spruce range and have several factors other than phenological differences that could affect insect performance. As with other plant species, many morphological and physiological traits vary among widely separated populations of white spruce (Wilkinson et al. 1971, Nienstaedt and Teich 1972, Nienstaedt 1985, Khalil 1986). The BC seed source is from a spruce hybrid zone in the western part of the white spruce range and may be affected by introgression with Engelmann spruce. Variation in susceptibility to insects among rangewide spruce seed sources has been recorded for the eastern spruce gall adelgid (*Adelges abietis*

(L.)) on white spruce (Canavera and DiGennaro 1979) and the green spruce aphid (*Elatobium abietinum* (Walker)) on Sitka spruce (Day 1984).

Effects of Tree Growth Rate

Despite the many inherent differences possible among the seed sources, a single variable, tree growth rate, appeared to account for much of the seed source effect that was not due to phenological differences. As noted above, a significant seed source effect still existed for length of development in days, growth rate and adult weight of budworms even after phenological differences were removed. These three variables were strongly associated with tree growth rate. Length of budworm development in days was negatively correlated and budworm growth rate and adult weight were positively correlated with tree growth rate (Figures 11, 12 and 13). These relationships existed for insects that were placed on host trees prior to budbreak, but not for those placed on trees during the time of budbreak.

One possible explanation of the effect of tree growth rate on insect performance is competition within the host tree for allocation of resources to growth and differentiation processes. Plants that are differentiation-dominated are inherently slow-growing and adapted to resource-limited environments. They generally have tougher, less digestible tissues owing to higher levels of cellulose and lignin and defensive compounds such as polyphenols and terpenoids (Coley et al. 1985, Bazzaz et al. 1987, Coley 1987, 1988, Loehle 1988). The SASK trees had the slowest growth rates and are probably adapted to drier sites than are trees of the other seed sources in this study. The relative growth rates of the seed sources correspond to the relative amounts of average annual rainfall at their sites of origin. Annual rainfall was reported by Nienstaedt (1963) to be 28 cm/yr for the

SASK seed source (slowest-growing), 50 cm/yr for the BC seed source, and 85 cm/yr for the ONT seed source (fastest-growing).

Temporal variation in the allocation of resources may explain why tree growth rate affected insects that began feeding prior to budbreak, but did not significantly affect those that began feeding during budbreak. The proportions of plant resources allocated to growth and to differentiation vary seasonally (Mooney et al. 1983, Lorio 1986, 1988). Allocation of resources to purely growth processes is highest in the early spring. Later, as new leaves finish growing, differentiation processes dominate and more resources are allocated for maturation and defenses. Budworms that started feeding prior to budbreak completed larval development during the period of active shoot growth. Those that started feeding during budbreak completed development at or shortly after the end of shoot elongation. It is possible that this latter group was exposed to less digestible and better defended tissues for a longer period.

Therefore, insects placed on trees during or after budbreak would encounter much less suitable food resources during their later larval stages. But, these are the crucial stages in which the greatest increases in body weight occur (Retnakaran 1983). Plant maturation processes that reduce the digestibility of foliage would be expected to negatively affect folivore weight gain and growth rate and to increase time of development. These are, in fact, the budworm performance variables most affected by tree growth rate.

Relationship of Host Susceptibility to Host Phenology

Results of canonical correlation and regression analyses both suggest that budworm performance is positively correlated with foliar levels of total sugar, nitrogen, phosphorous, potassium and water, and negatively correlated with

calcium and leaf toughness. Because of the intercorrelation among many of these foliar traits, it is difficult in a field study such as this to "tease out" and identify key factors affecting host susceptibility. However, several strong, consistent relationships do exist.

Comparison of the timing of changes in budworm performance and changes in levels of foliar traits can be used to identify potential relationships. The greatest reductions in larval survival occur during early larval stages. At this time, nitrogen, phosphorous, water and toughness are the foliar traits that exhibit the greatest variation and, therefore, could be considered as a suite of candidates for key factors affecting larval survival. Most of larval weight gain occurs during the last larval stage (Retnakaran 1983). At this time, phosphorous, potassium, calcium, water and toughness are the foliar traits that have the greatest variation and, therefore, could be considered as a suite of candidates for key factors affecting weight gain. However, the magnitude of effect that changes in foliar quality have on budworm performance may vary with larval age. For example, one hypothesis states that the performance of young larvae tends to be much more sensitive to changes in host quality than is that of older larvae (Scriber and Slansky 1981, White 1984).

Key Foliar Traits

Total Sugars -- The levels of total sugars in new foliage were highest near the middle of the shoot elongation period. This pattern is consistent with earlier observations of foliar sugars in white spruce (McLaughlin 1986) and balsam fir (Little 1970). A weak positive relationship exists between budworm performance and levels of total sugars. Sugars are potent feeding stimulants for spruce budworm larvae (Heron 1965, Albert and Jerrett 1981, Albert 1982, Albert et al. 1982, Albert and Parisella 1985). Budworm weight and development rate increase

as dietary levels of sugars increase to an optimal level (Harvey 1974; McLaughlin 1986; F. Lo, unpublished data). Harvey (1974) determined that glucose, fructose and sucrose (the most common sugars of current-year foliage in conifers) have equivalent nutritional value for the spruce budworm. Thus, from a nutritional point of view, the total amount of sugars are probably more important than the proportion of individual sugars.

Foliar levels of sugars in this study were adequate for budworm development in all cohorts. It is not likely that variation in sugar levels was a major determinant of variation in budworm performance among cohorts. However, increased sugar levels during shoot growth may have elicited increased larval feeding in the early cohorts.

Nitrogen -- Quantitative variation in nitrogen followed the pattern typical of most plants (Mattson 1980, Mattson et al. 1983, Mattson and Scriber 1987). Nitrogen levels were highest in swelling buds and decreased rapidly during early shoot growth. The importance of nitrogen to insect performance has been well documented for many phytophagous insects (McNeill and Southwood 1978, Mattson 1980, Scriber and Slansky 1981, Scriber 1984a, 1984b, White 1984, Mattson and Scriber 1987) as well as for spruce budworms specifically (Harvey 1974, Mattson et al. 1983, Montgomery and Czapowskyj 1985, Brewer et al. 1985, 1987, McLaughlin 1986, Cates et al. 1987, Mattson et al. 1990).

Budworm performance was strongly correlated with nitrogen levels, particularly with levels occurring during early larval development. Larval survival was positively correlated with nitrogen levels during early larval development up to ca. 2.5% to 3% (dw) for total nitrogen. Only a few observations were available at higher nitrogen levels, but generally larval survival did not increase with higher levels. Similarly, Brewer et al. (1985, 1987) reported that performance of the

western spruce budworm peaked at foliar nitrogen levels of 2.4% to 2.5% and decreased at both higher and lower levels.

Nitrogen in plant tissue varies qualitatively as well as quantitatively during a growing season. Young tissue has higher levels of amino acids, soluble proteins and nitrogen-based secondary compounds, while older tissue has higher levels of structural or insoluble protein (Mattson 1980). Seasonal variation of several amino acids in white spruce foliage has been documented (Durzan 1968). L-proline and amino acid/base fractions of foliage from white spruce and other host species have been shown to be mild feeding stimulants for the spruce budworm (Heron 1965, Albert 1982, Albert and Parisella 1985). Arginine is the foliar amino acid that makes up the largest portion of protein in budworm larvae, although it does not act as a feeding stimulant itself (Heron 1965, Durzan and Lopushanski 1968).

Minerals -- Seasonal variation among mineral elements was consistent with patterns observed in other conifers (Chapin and Kedrowski 1983, Clancy et al. 1988a, Hockman et al. 1989) and most other plants (Mattson and Scriber 1987). Among the mineral elements measured, increased budworm performance was most closely correlated with increased levels of phosphorous, potassium and zinc and with decreased levels of calcium. The pattern of variation of phosphorous is an exponential decrease during the growing season that closely follows the change in levels of nitrogen. Thus, the same phenological relationships existing between budworm performance and nitrogen also exist for budworm performance and phosphorous. Potassium decreases at a slower rate during the growing season than do nitrogen and phosphorous, and therefore budworm performance was more closely associated with levels of potassium during late larval development rather than early larval development. Budworm performance was positively

associated with zinc levels during early larval development and negatively associated with calcium levels during late larval development.

Little information is available on the levels of mineral elements in insect tissues and the dietary requirements of insects for mineral elements. However, results of most studies indicate that phosphorous, potassium and magnesium are the dominant mineral elements in insect tissues (Mattson and Scriber 1987). Phosphorous, copper, zinc, iron and sodium in spruce budworms (Mattson et al. 1983) and copper and zinc in western spruce budworms (McLean et al. 1983) have been measured at levels that are at least twice that of host tree foliage.

Water -- Water content of current-year foliage peaked at more than 80% soon after budbreak and decreased to less than 60% by early July. Chrosciewicz (1986) observed a nearly identical pattern for white spruce and similar patterns with slightly lower peaks for balsam fir, black spruce and jack pine (*Pinus banksiana* Lamb.). Budworm performance in this study was highly correlated with water content of foliage during both early and late larval development. The positive relationship between leaf water content and the performance of folivorous insects has been well documented for many insect species (Scriber 1977, 1978, Scriber and Slansky 1981, Scriber 1984b).

The general trend of decreasing water content in maturing foliage occurs in most, if not all, plants (Scriber 1984b). It is closely correlated with declining levels of nitrogen. Because of the consistency in phenological variation in water and nitrogen levels, and their crucial roles in governing the course of plant physiology (Ågren 1985, McIntyre 1987), these two variables are valuable as indicators of the entire chemical and physiological "gestalt" of a host plant (Mattson and Scriber 1987).

Toughness -- Leaf toughness increased dramatically during shoot elongation and was strongly negatively correlated with decreased budworm

performance. Toughness is related to the levels of compounds that together comprise "fiber" (lignin, silica, pectin, cellulose, hemicellulose, etc.) and structural components such as sclerenchyma fibers and bundle sheaths (Huang 1975, Huang and Fuhrer 1979, Vincent 1982, Hagen and Chabot 1986, Mattson and Scriber 1987). Leaf toughness has frequently been associated with reduced levels of herbivory or reduced insect performance (Feeny 1970, Huang 1975, Huang and Fuhrer 1979, Coley 1983, Lowman and Box 1983, Raupp 1985, Hagen and Chabot 1986). Bauce and Hardy (1988) reported that increased rawfiber content of current-year foliage was related to previous defoliation of balsam fir and caused decreases in pupal weight, larval developmental rate and survival of spruce budworms.

Leaf toughness and water content are generally negatively correlated and together can be considered as a measure of sclerophylly (Lechowicz 1983). Seasonal variation of these two variables more clearly demonstrated the phenological differences among seed sources in this study than did any other foliar traits. Thus, leaf toughness and water content may be highly important factors that affect larval survival and length of development in degree days, i.e. those budworm performance variables that are associated with phenological differences among seed sources.

Secondary Compounds -- The potential role of secondary compounds was not evaluated in this study; however, the evidence available to date does not indicate a strong relationship between secondary compounds and resistance to the spruce budworm. Phenolic compounds seem to have little or no deleterious effect on spruce budworm or western spruce budworm performance at the levels found in host foliage (Cates et al. 1983a, 1983b, Mattson et al. 1983, Wagner and Blake 1983, Cates and Redak 1988). The role of foliar terpenes is less clear. In some cases budworm performance in field tests has been negatively correlated with

measures of various terpene levels during later larval instars, although the trends are inconsistent (Cates et al. 1983a, 1983b, Mattson et al. 1983, Cates and Redak 1988). Laboratory tests with artificial diet containing levels of monoterpenes comparable to those found in host foliage have had results that differ between insect species. Bornyl acetate concentrations were negatively correlated with western spruce budworm performance (Cates et al. 1987), but bornyl acetate and six other monoterpenes had little or no effect on spruce budworm performance (Mattson et al. 1990).

Foliar Traits of the Window of Susceptibility

The extent of the window of host susceptibility to the spruce budworm can be described in terms of temporal events (bud and shoot phenology, dates and degree days), as discussed above, and in terms of foliar traits. Ordination of canonical scores (Figures 22-24) provides one view of the extent of the window of susceptibility along a composite axis of foliar traits. The zero-point on the insect performance axis closely (and somewhat coincidentally) defines the window of white spruce susceptibility to the spruce budworm. Points located in the upper two quadrants of the ordination plots (Figures 22-24) lie within the window of susceptibility. These points include cohorts 1, 2 and part of 3 for the early-flushing SASK seed source and cohorts 1, 2, 3 and part of 4 for the ONT and BC seed sources. The lower limit of the window of susceptibility in terms of foliar traits corresponds to a value of ca. -0.3 on the host quality axis.

A multi-dimensional estimate of the window of susceptibility can be constructed by examining the ranges of individual foliar traits for which the herbivore can successfully survive and grow (Mattson et al. 1982). A summary of ranges of foliar trait values associated with points in the upper quadrants of the ordination plots (Figures 22-24) provides a 13-dimensional estimate of the window

of white spruce susceptibility to the spruce budworm (Table 19). The ranges of most foliar trait values within the window of susceptibility are comparable to optimal dietary levels that have been estimated for the spruce budworm (Harvey 1974, Mattson and Koller 1983) and other folivorous Lepidoptera (Mattson and Scriber 1987). One exception is the level of calcium which is 4 to 17 times greater than the estimated minimally optimal level (Mattson and Scriber 1987).

A two-dimensional foliar trait space has often been used to describe insect herbivore-host plant relationships. Foliar levels of nitrogen and water are good indicators of relative growth rate and approximate digestibility for many insect herbivores (Scriber and Slansky 1981, Scriber 1984a, 1984b). Foliar levels of nitrogen and water that existed during early larval development accurately define the window of white spruce susceptibility to the spruce budworm (Figure 32). Larval survival was highest when water content was greater than 75% and the level of total nitrogen was greater than 2%. A clear relationship is also demonstrated for leaf water content and toughness (Figure 33), the two foliar traits likely to be the key factors in determining white spruce susceptibility to the spruce budworm. Larval survival was greatest when water content and toughness during early larval development were greater than 75% and less than 200 g, respectively.

Effects of Insect-Tree Phenological Asynchrony

When spruce budworm phenology is too advanced in relation to host tree phenology, the 2nd-stage larvae must remain on older foliage for an extended period prior to budbreak. Older foliage clearly has lower nutritional value (Table 15 and Mattson et al. 1983). Nutrient levels in one-year-old foliage in early spring are in many cases similar to values existing at the end of summer for current-year foliage. Moreover, water content is even lower than the end-of-summer levels.

Table 19. Range of values for foliar traits during early larval development and late larval development within the phenological window of susceptibility.

Foliar Trait	Units	Early Larval Development	Late Larval Development
Total Sugar	% dw	11.6 - 17.4	9.80 - 16.7
Nitrogen	% dw	1.70 - 5.84	1.12 - 2.12
Phosphorous	mg/g dw	2.47 - 9.94	1.67 - 3.88
Potassium	mg/g dw	10.9 - 20.7	10.9 - 19.9
Calcium	mg/g dw	1.43 - 5.18	1.27 - 3.47
Magnesium	mg/g dw	1.05 - 1.89	0.98 - 1.48
Manganese	mg/g dw	0.225 - 0.833	0.233 - 0.946
Copper	μg/g dw	5.14 - 17.14	4.35 - 10.20
Iron	μg/g dw	24.5 - 42.4	20.3 - 43.4
Sodium	μg/g dw	24.1 - 80.7	18.0 - 48.7
Zinc	μg/g dw	41.6 - 72.1	30.7 - 57.8
Water Content	% fw	71.7 - 82.8	65.9 - 81.8
Toughness	g	5.0 - 263.0	27.0 - 802.0

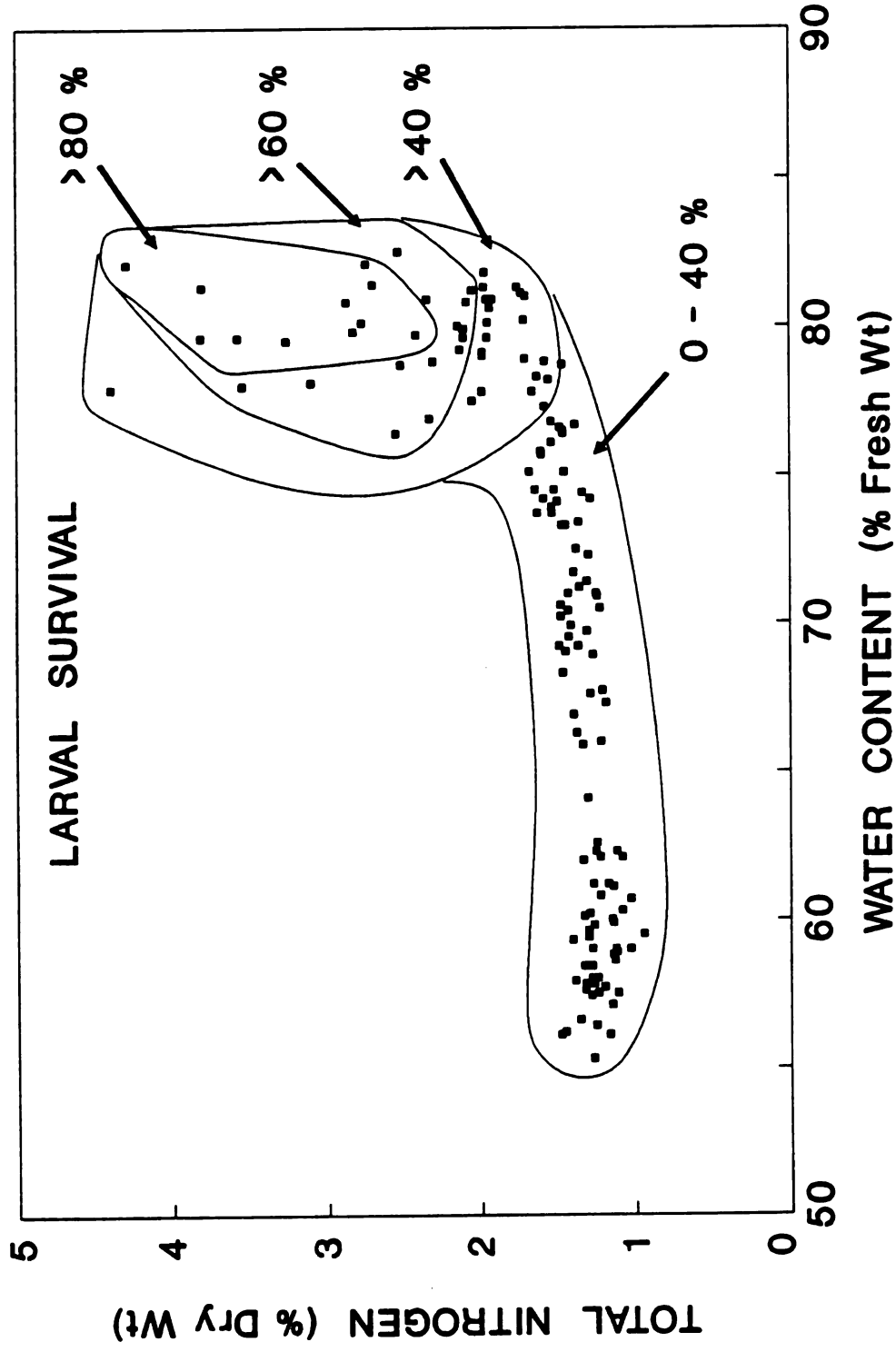

Figure 32. Relationship of percent larval survival and foliar levels of total nitrogen and water during early larval development.

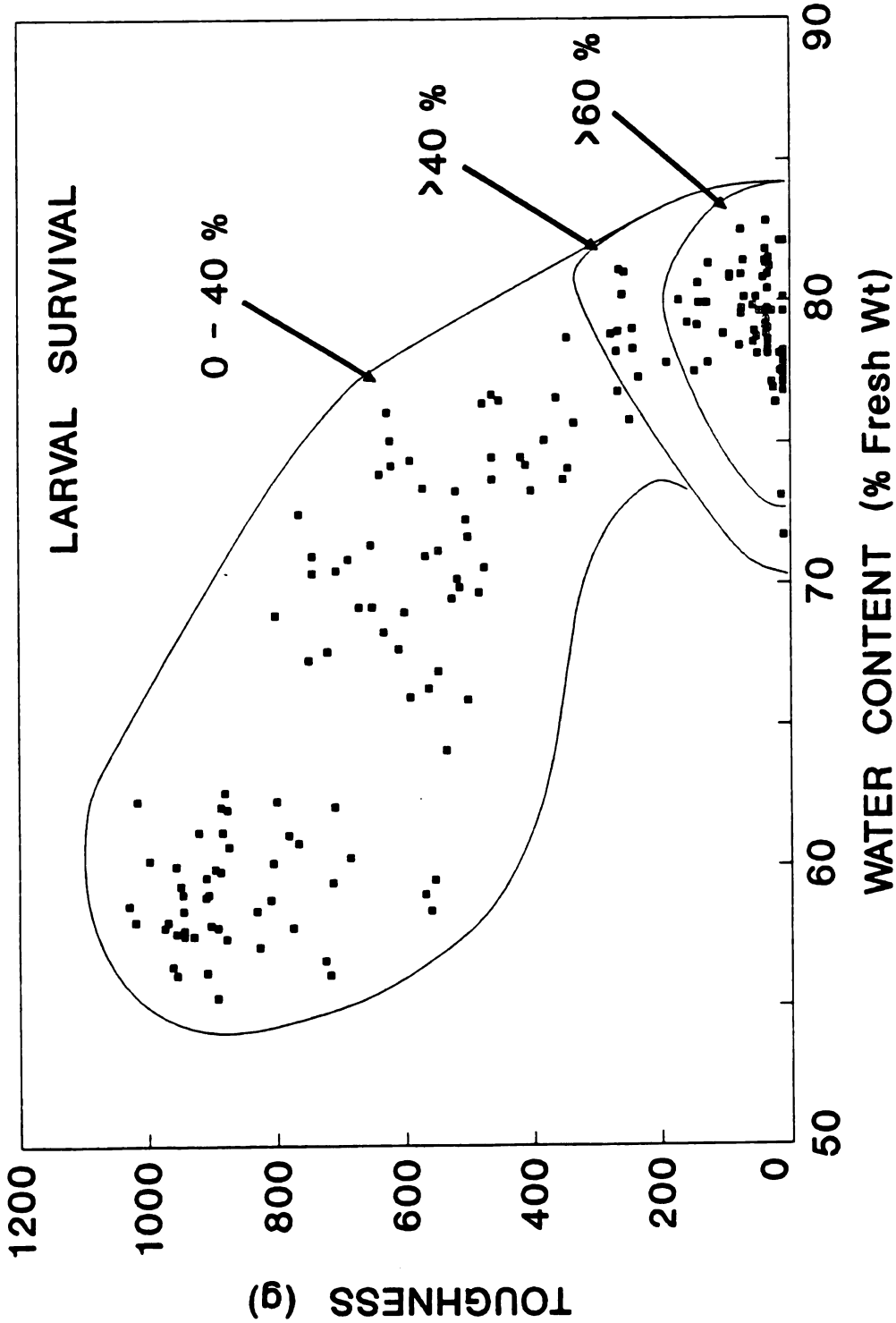

Figure 33. Relationship of percent larval survival and foliar levels of toughness and water during early larval development.

One cause of larval mortality during this period is increased larval dispersal as larvae search for suitable feeding sites (Beckwith and Burnell 1982). In this study, where larvae were caged on branches and prevented from dispersing, the typical pattern of high mortality levels among young larvae still existed. Thus, I hypothesize that extended feeding on poor nutritional quality diets is also a major cause of young larval mortality.

When spruce budworm phenology is retarded in relation to host tree phenology, reduced budworm performance is obvious for many performance variables. Survival, growth rates and weights are dramatically reduced. Increased development time allows an increased period of exposure to predators. Decreased body weight is correlated with decreased fecundity (Miller 1957). Larvae feeding on older current-year foliage generally have a higher relative consumption rate, a lower relative growth rate and lower efficiency of food utilization (Blake and Wagner 1986, Thomas 1987, 1989).

Implications for Forest Pest Management

The results of this study impact on at least two areas of forest pest management: modelling pest population dynamics and tree improvement strategies. Although numerous models of spruce budworm and western spruce budworm population dynamics have been developed in recent years (Simmons et al. 1984, Sheehan et al. 1989), better understanding of the effects of insect-host asynchrony on budworm survival and fecundity is needed, because it will allow more precise modelling of budworm population fluctuations. Models could be developed that describe temperature effects on the levels of insect-host asynchrony, the phenological limits of the windows of susceptibility for all host tree species and the effects of varying levels of asynchrony on budworm survival

and fecundity. Much of the data required for a spruce budworm-white spruce phenological synchrony model has been provided by this study.

The effects of seed source differences in phenology and growth rate on spruce budworm performance have important implications for future tree breeding strategies. White spruce is a popular species in tree improvement programs in north central and northeastern United States and throughout Canada (e.g. Bongarten and Hanover 1982, Carter and Simpson 1985, Rauter 1985, Fowler 1986, Nienstaedt and Kang 1987, Fowler and Morgenstern 1990). However, reduced interest in planting white spruce in some areas has resulted from, among other reasons, the susceptibility of white spruce to damage from the spruce budworm and damage from late spring frosts (Rauter 1985, Blum 1988). Breeding for delayed budbreak has been suggested as both a method of inducing budworm-tree asynchrony, and thereby increasing resistance to the spruce budworm (Blum 1988), and as a method to reduce damage due to spring frosts (Nienstaedt and King 1970, Nienstaedt 1985).

Breeding for delayed budbreak may not be a practical solution to these problems. Nienstaedt (1985) and Blum (1988) concluded that some gain in lateness of budbreak could be achieved, although it would be costly. It is also questionable whether enough gain could be achieved to overcome the phenological plasticity of the spruce budworm. In my study, budworms were able to perform well even when budbreak occurred three to four weeks after the larvae were placed on the trees. Other studies indicate that there is wide variability within and among populations of the spruce budworm and the western spruce budworm for rates of spring emergence in response to temperature (Rose and Blais 1954, Thomas 1976, Volney et al. 1983, Volney 1985).

Based on the results of my study, it might be suggested that advancing the host window, rather than delaying it, may be more effective in reducing

susceptibility to the budworm. The end of the phenological window is very abrupt, and reduction in budworm performance is dramatic. However, advancing the end of the window, would involve selecting for an earlier date of growth cessation, a trait that is controlled largely by photoperiod (Nienstaedt 1974), and may result in the undesirable trait of reduced tree height growth.

Loehle and Namkoong (1987) have raised another concern, i.e. that breeding for increased growth rate may adversely affect defensive capabilities of trees. Resources that are allocated within the tree to growth are not available for defense or other differentiation processes (Coley et al. 1985, Bazzaz et al. 1987, Coley 1988, Loehle 1988). The positive relationship between tree growth rate and spruce budworm performance in my study supports this hypothesis. In contrast, apparent negative relationships between tree growth rate and insect performance exist for some other herbivore guilds, e.g. bark beetles (Hard 1985). However, negative relationships involving bark beetles are largely based on phenotypic variation in tree vigor and growth rates in response to variation in forest stand density (Mitchell et al. 1983, Hard 1985, Matson et al. 1987). Further studies are needed to determine the roles that genotypic variation in tree growth rates and seasonal variation in tree growth-differentiation relationships (see Lorio 1988) play in tree susceptibility to bark beetles. Nevertheless, the results of my study underscore the need for caution in tree breeding programs when selections are based primarily on tree growth traits.

Recommendations for Future Research

There are several areas where we lack the knowledge required to fully develop models of budworm-tree synchrony. Comprehensive studies should be undertaken to determine the phenological windows in other host tree species

(balsam fir, red spruce, black spruce). More detailed information is needed about the role of phenological windows in the differential susceptibility of host tree species. Regniere (1987) has suggested several areas in which we lack fundamental knowledge about budworm and host tree phenology -- e.g. mechanisms controlling budworm diapause termination, variability in budworm responses to temperature and developmental responses of larvae feeding on old foliage and various host species. A more detailed examination of the plasticity of spring emergence rates among and within budworm populations should be done prior to large investments in breeding programs for delayed budbreak.

A better understanding is needed of the allocation of resources to tree growth and differentiation processes as it relates to tree susceptibility to the spruce budworm. What are the mechanisms causing reduced performance of asynchronous budworms? Sclerophylly (tough leaves with low water content) appears to be the major factor reducing budworm performance in my study. Are there specific defensive compounds produced by host trees that also reduce budworm performance? If so, patterns of phenological variation of such compounds and their roles in the competitive allocation of resources need to be determined.

CONCLUSIONS

1. White spruce has a sharply defined phenological window of susceptibility to the spruce budworm, a period of about eight weeks in Michigan.

2. The phenological window for successful development of the spruce budworm commences about three weeks prior to budbreak and ends at the cessation of shoot elongation. Spruce budworm performance was also high for cohorts that started feeding as early as four weeks prior to budbreak and no later than budbreak. Total performance was best for those insects that started feeding two weeks prior to budbreak. Larvae that began during this period were able to complete larval development prior to the end of shoot elongation.

3. At least a few spruce budworms were able to survive and develop to adults during all test periods between late April and early September, demonstrating the physiological plasticity within the species.

4. Variation among white spruce seed sources in their suitability for larval survival and length of development (degree days) was clearly linked to their differences in phenology.

5. Variation among white spruce seed sources in their suitability for total budworm growth, growth rate and length of development (days) was clearly linked to tree growth rate. Competition within host trees for allocation of resources to growth processes and to maturation and defense processes may explain the effect of tree growth rate.

6. Although budworm survival was much higher in April-June, budworms developing in June-July had the same survivorship curve: more than 85% of total larval mortality occurred by the time most surviving larvae were 3rd instars.

7. When young larvae were placed on trees three to four weeks prior to budbreak, the majority of them fed on old foliage. On the other hand, when young larvae were placed on trees at about three weeks after budbreak, they fed almost exclusively on current-year foliage. The latter group was observed mining new needles in the manner typical of larvae mining old needles in early spring.

8. Increased budworm performance was most strongly correlated with higher foliar levels of water and lower levels of leaf toughness. Water content and leaf toughness were the two foliar traits that most closely reflected the relative differences in timing of phenology among the three white spruce seed sources. Together, these two foliar traits represent a measure of sclerophylly and are likely to be the key factors that define the phenological window of susceptibility.

9. Among the other foliar traits, increased budworm performance was strongly correlated with higher levels of total nitrogen and phosphorous. Weaker positive relationships existed between budworm performance and higher levels of total sugars, potassium and zinc and lower levels of calcium.

10. In some cases the relationship between budworm performance and foliar traits differed between foliar levels present during early larval development and the levels of the same traits present during late larval development. For example, budworm performance was more closely correlated with early than late foliar levels of total nitrogen, phosphorous, zinc and toughness. On the other hand, performance was more closely correlated with late than early foliar levels of potassium and calcium.

APPENDIX

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1988-03

Title of thesis or dissertation (or other research projects):

Phenological Variation in the Susceptibility of White Spruce to the Spruce Budworm

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums: None

Investigator's Name (s) (typed)

Robert K. Lawrence

Date 27 July 1990

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Choristoneura fumiferana (Clemens)	Sault Ste. Marie, Ontario, Canada Lab Culture, April 1987		40		10	5	5		MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Robert K. Lawrence

Date 27 July 1990

Voucher No. 1988-03

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Richard W. Fischer 7 August 1990

Curator Date

LITERATURE CITED

LITERATURE CITED

Ågren, G.I. 1985. Theory for growth of plants derived from the nitrogen productivity concept. Physiol. Plant. 64: 17-28.

Albert, P.J. 1982. Host plant preferences in larvae of the eastern spruce budworm, *Choristoneura fumiferana*. p. 19-24. Proc. 5th Int. Symp. Insect-Plant Relationships. Pudoc, Wageningen.

Albert, P.J., C. Cearley, F. Hanson and S. Parisella. 1982. Feeding responses of eastern spruce budworm larvae to sucrose and other carbohydrates. J. Chem. Ecol. 8: 233-239.

Albert, P.J. and P.A. Jerrett. 1981. Feeding preferences of spruce budworm (*Choristoneura fumiferana* Clem.) larvae to some host-plant chemicals. J. Chem. Ecol. 7: 391-402.

Albert, P.J. and S. Parisella. 1985. Feeding preferences of eastern spruce budworm larvae in two-choice tests with combinations of host-plant extracts. Ent. Exp. Appl. 38: 221-225.

Allen, J.C. 1976. A modified sine wave method for calculating degree days. Environ. Ent. 5: 388-396.

Baldwin, I.T., J.C. Schultz and D. Ward. 1987. Patterns and sources of leaf tannin variation in yellow birch (*Betula allegheniensis*) and sugar maple (*Acer saccharum*). J. Chem. Ecol. 13: 1069-1078.

Bauce, E. and Y. Hardy. 1988. Effects of drainage and severe defoliation on the rawfiber content of balsam fir needles and growth of the spruce budworm (Lepidoptera: Tortricidae). Environ. Ent. 17: 671-674.

Bazzaz, F.A., N.R. Chiariello, P.D. Coley and L.F. Pitelka. 1987. Allocating resources to reproduction and defense. BioSci. 37: 58-67.

Bean, J.L. 1961. Predicting emergence of second-instar spruce budworm larvae from hibernation under field conditions in Minnesota. Ann. Ent. Soc. Amer. 54: 175-177.

Bean, J.L. and H.O. Batzer. 1957. Mean head width for spruce budworm larval instars in Minnesota and associated data. J.Econ. Ent. 50: 499.

Beckwith, R.C. and D.G. Burnell. 1982. Spring larval dispersal of the western spruce budworm (Lepidoptera: Tortricidae) in north-central Washington. Environ. Ent. 11: 828-832.

Bernard-Dagan, C. 1988. Seasonal variations in energy sources and biosynthesis of terpenes in maritime pine. p. 93-116. In: W.J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.) Mechanisms of Woody Plant Defenses Against Insects -- Search for Pattern. Springer-Verlag, New York.

Blais, J.R. 1957. Some relationships of the spruce budworm, *Choristoneura fumiferana* (Clem.), to black spruce, *Picea mariana* (Moench) Voss. For. Chron. 33: 364-372.

Blais, J.R. 1979. Rate of defoliation of balsam fir in relation to spruce budworm attack and timing of spray application. Can. J. For. Res. 9: 354-361.

Blake, E.A. and M.R. Wagner. 1986. Foliage age as a factor in food utilization by the western spruce budworm, *Choristoneura occidentalis*. Great Basin Nat. 46: 169-172.

Blum, B.M. 1988. Variation in the phenology of bud flushing in white and red spruce. Can. J. For. Res. 18: 315-319.

Bongarten, B.C. and J.W. Hanover. 1982. Hybridization among white, red, blue, and white x blue spruces. For. Sci. 28: 129-134.

Brewer, J.W., J.L. Capinera, R.E. Deshon, Jr. and M.L. Walmsley. 1985. Influence of foliar nitrogen levels on survival, development, and reproduction of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae). Can. Ent. 117: 23-32.

Brewer, J.W., K.M. O'Neill and R.E. Deshon, Jr. 1987. Effects of artificially altered foliar nitrogen levels on development and survival of young instars of western spruce budworm, *Choristoneura occidentalis* Freeman. J. Appl. Ent. 104: 121-130.

Cameron, D.G., G.A. McDougall and C.W. Bennett. 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Ent. 61: 857-858.

Canavera, D.S. and J. DiGennaro. 1979. Characteristics of eastern spruce gall aphid attack among 24 white spruce seed sources in central Maine. Proc. Northeast. For. Tree Improv. Conf. 26: 96-101.

Carter, K.K. and J.D. Simpson. 1985. Status and outlook for tree improvement programs in the Northeast. North. J. Appl. For. 2: 127-131.

Cates, R.G. 1987. Influence of biological rhythms, tissue development, and physiological state of plants and insects on their interactions. p. 175-182. In: V. Labeyrie, G. Fabres and D. Lachaise (eds.) Insects - Plants. Dr. W. Junk Publ., Dordrecht, Netherlands.

Cates, R.G., C.B. Henderson and R.A. Redak. 1987. Responses of the western spruce budworm to varying levels of nitrogen and terpenes. Oecologia 73: 312-316.

Cates, R.G. and R.A. Redak. 1988. Variation in the terpene chemistry of Douglas-fir and its relationship to western spruce budworm success. p. 317-344. In: K.C. Spencer (ed.) Chemical Mediation of Coevolution. Acad. Press, San Diego, Calif.

Cates, R.G., R. Redak and C.B. Henderson. 1983a. Natural product defensive chemistry of Douglas-fir, western spruce budworm success, and forest management practices. Z. Ang. Ent. 96: 173-182.

Cates, R.G., R. Redak and C.B. Henderson. 1983b. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. p. 3-19. In: P.A. Hedin (ed.) Plant Resistance to Insects. Amer. Chem. Soc., Wash., D.C.

Chapin, F.S., III, and R.A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorous fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64: 376-391.

Chapin, F.S., III, J.D. McKendrick, and D.A. Johnson. 1986. Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: Implications for herbivory. J. Ecol. 74: 707-731.

Chrosciewicz, Z. 1986. Foliar moisture content variations in four coniferous tree species of central Alberta. Can. J. For. Res. 16: 157-162.

Chung, H. and R.L. Barnes. 1980. Photosynthate allocation in *Pinus taeda*. II. Seasonal aspects of photosynthate allocation to different biochemical fractions in shoots. Can. J. For. Res. 10: 338-347.

Clancy, K.M., M.R. Wagner and R.W. Tinus. 1988a. Variation in host foliage nutrient concentrations in relation to western spruce budworm herbivory. Can. J. For. Res. 18: 530-539.

Clancy, K.M., M.R. Wagner and R.W. Tinus. 1988b. Variation in nutrient levels as a defense: Identifying key nutritional traits of host plants of the western spruce budworm. p. 203-213. In: W.J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.) Mechanisms of Woody Plant Defenses Against Insects -- Search for Pattern. Springer-Verlag, New York.

Clark, E.W., J.D. White and E.L. Bradley. 1975. Seasonal changes in foliar fatty acids and sterols in *Carya glabra* (Mill.) Sweet and *Quercus falcata* Michx., two hosts of the elm spanworm, *Ennomos subsignarius* (Hübner). Environ. Ent. 4: 935-943.

Cleary, B.D. and R.H. Waring. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. 47: 167-173.

Cole, J.W.L. and J.E. Grizzle. 1966. Applications of multivariate analysis of variance to repeated measurements experiments. Biometrics 22: 810-828.

Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53: 209-233.

Coley, P.D. 1987. Between-species differences in leaf defenses of tropical trees. p. 30-35. In: F.D. Provenza, J.T. Flinders and E.D. McArthur (eds.) Proc. Sympos. on Plant-Herbivore Interactions. USDA For. Serv. Gen. Tech. Rept. INT-222.

Coley, P.D. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74: 531-536.

Coley, P.D., J.P. Bryant, F.S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899.

Crummey, H.R. and I.S. Otvos. 1980. Biology and habits of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) in Newfoundland. Environ. Canada, Newfoundland For. Res. Ctr. Info. Rept. N-X-181, 33p.

Danford, M.B., H.M. Hughes and R.C. McNee. 1960. On the analysis of repeated-measurements experiments. Biometrics 16: 547-565.

Davidson, M.L. 1972. Univariate versus multivariate tests in repeated-measures experiments. Psychol. Bull. 77: 446-452.

Day, K. 1984. Systematic differences in the population density of green spruce aphid, *Elatobium abietinum*, in a provenance trial of Sitka spruce, *Picea sitchensis*. Ann. Appl. Biol. 105: 405-412.

Du Merle, P. 1988. Phenological resistance of oaks to the green oak leafroller, *Tortrix viridana* (Lepidoptera: Tortricidae). p. 215-226. In: W.J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.) Mechanisms of Woody Plant Defenses Against Insects -- Search for Pattern. Springer-Verlag, New York.

Durzan, D.J. 1968. Nitrogen metabolism of *Picea glauca*. I. Seasonal changes of free amino acids in buds, shoot apices, and leaves, and the metabolism of uniformly labelled ^{14}C-L-arginine by buds during the onset of dormancy. Can. J. Bot. 46: 909-919.

Durzan, D.J. and S.M. Lopushanski. 1968. Free and bound amino acids of spruce budworm larvae feeding on balsam fir and red and white spruce. J. Insect Physiol. 14: 1485-1497.

Eidt, D.C. and M.D. Cameron. 1971. Delayed budbreak and spruce budworm survival. Can. For. Serv. Bi-Mon. Res. Notes 27(4): 28-29.

Eidt, D.C. and C.H.A. Little. 1970. Insect control through induced host-insect asynchrony: A progress report. J. Econ. Ent. 63: 1966-1968.

Embree, D.G. 1965. The population dynamics of the winter moth in Nova Scotia, 1954-1962. Mem. Ent. Soc. Can. 46, 57p.

Ericsson, A. 1978. Seasonal changes in translocation of ^{14}C from different age-classes of needles on 20-year-old Scots pine trees (*Pinus silvestris*). Physiol. Plant. 43: 351-358.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565-581.

Feeny, P. 1976. Plant apparency and chemical defense. Rec. Adv. Phytochem. 10: 1-40.

Fowells, H.A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Agric. Hdbk. 271, 762p.

Fowler, D.P. 1986. Strategies for the genetic improvement of important tree species in the Maritimes. Can. For. Serv. - Maritimes, Info. Rept. M-X-156, 30p.

Fowler, D.P. and E.K. Morgenstern. 1990. Tree improvement research and development in Canada. For. Chron. 66: 97-101.

Genys, J.B. and H. Nienstaedt. 1979. Variation in white spruce from 24 different provenances studied in Maryland's piedmont plateau. Proc. Northeast. For. Tree Improv. Conf. 26: 48-57.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. I. The role of climate. Can. J. Zool. 34: 453-476.

Greenbank, D.O. 1963. Host species and the spruce budworm. p. 219-223. In: R.F. Morris (ed.) The Dynamics of Epidemic Spruce Budworm Populations. Mem. Ent. Soc. Can., No. 31.

Grigal, D.F., L.F. Ohmann and R.B. Brander. 1976. Seasonal dynamics of tall shrubs in northeastern Minnesota: Biomass and nutrient element changes. Forest Sci. 22: 195-208.

Haack, R.A., R.K. Lawrence and W.J. Mattson. 1991. Impact of root pruning on white spruce and its herbivore the spruce budworm. In peer review.

Hagen, R.H. and J.F. Chabot. 1986. Leaf anatomy of maples (*Acer*) and host use by Lepidoptera larvae. Oikos 47: 335-345.

Hanover, J.W. and D.A. Reicosky. 1971. Surface wax deposits on foliage of *Picea pungens* and other conifers. Amer. J. Bot. 58: 681-687.

Hard, J.S. 1985. Spruce beetles attack slowly growing spruce. For. Sci. 31: 839-850.

Hardy, Y., M. Mainville and D.M. Schmidt. 1986. An atlas of spruce budworm defoliation in eastern North America, 1938-80. USDA For. Serv. Misc. Pub. 1449, 52p.

Harvey, G.T. 1958. A relationship between photoperiod and cold-storage treatment in the spruce budworm. Science 128: 1205-1206.

Harvey, G.T. 1974. Nutritional studies of eastern spruce budworm (Lepidoptera: Tortricidae) I. Soluble sugars. Can. Ent. 106: 353-365.

Harvey, G.T. 1985. The taxonomy of the coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A review. p. 16-48. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Haukioja, E., P. Niemela, L. Iso-Iivari, H. Ojala and E. Aro. 1978. Birch leaves as a resource for herbivores. I. Variation in the suitability of leaves. Rep. Kevo Subarctic Res. Stat. 14: 5-12.

Henson, W.R. 1948. Influence of meteorological factors on behaviour of the spruce budworm. Domin. Dept. Agric.; Sci. Serv.--Div. Ent.; Ottawa, Canada; For. Insect Invest. Bi-Mon. Prog. Rept. 4(6): 2.

Heron, R.J. 1965. The role of chemotactic stimuli in the feeding behavior of spruce budworm larvae on white spruce. Can. J. Zool. 43: 247-269.

Hinckley, T.M., J.P. Lassoie and S.W. Running. 1978. Temporal and spatial variations in the water status of forest trees. For. Sci. Monogr. 20, 72p.

Hockman, J.N., J.A. Burger and D.W. Smith. 1989. Spatial and temporal variability of foliar nutrient levels in Fraser fir Christmas trees. For. Sci. 35: 632-639.

Huang, P. 1975. Relationship between the needle structure of *Picea excelsa* and the behaviour of some needle eating insect species. Z. Ang. Ent. 77: 264-269.

Huang, P. and E. Fuhrer. 1979. As to food quality of spruce needles for forest damaging insects. 12. Variation in epidermis and hypodermis structure. Z. Ang. Ent. 88: 231-245.

Khalil, M.A.K. 1985. Genetic variation in eastern white spruce (*Picea glauca* (Moench) Voss) populations. Can. J. For. Res. 15: 444-452.

Khalil, M.A.K. 1986. Variation in seed quality and some juvenile characters of white spruce (*Picea glauca* (Moench) Voss). Silvae Gen. 35: 78-85.

Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of woody plants. Acad. Press, Orlando, Fla., 811p.

Krischik, V.A. and R.F. Denno. 1983. Individual, population, and geographic patterns in plant defense. p. 463-512. In: R.F. Denno and M.S. McClure (eds.) Variable Plants and Herbivores in Natural and Managed Systems. Acad. Press, New York.

LaTour, S.A. and P.W. Miniard. 1983. The misuse of repeated measures analysis in marketing research. J. Marketing Res. 20: 45-57.

Lavender, D.P., G.B. Sweet, J.B. Zaerr and R.K. Hermann. 1973. Spring shoot growth in Douglas-fir may be initiated by gibberellins exported from the roots. Science 182: 838-839.

Lawton, J.H. and S. McNeill. 1979. Between the devil and the deep blue sea: On the problem of being a herbivore. Symp. Brit. Ecol. Soc. 20: 223-244.

Leather, S.R. 1986. The effect of neonatal starvation on the growth, development and survival of larvae of the pine beauty moth, *Panolis flammea* (D. & S.). Oecologia 71: 90-93.

Lechowicz, M.J. 1983. Leaf quality and the host preferences of gypsy moth in the northern deciduous forest. p. 67-82. In: R.L. Talerico and M. Montgomery (eds.) Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. USDA For. Serv. Gen. Tech. Rept. NE-85.

Little, C.H.A. 1970. Seasonal changes in carbohydrate and moisture content in needles of balsam fir (*Abies balsamea*). Can. J. Bot. 48: 2021-2028.

Loach, K. and C.H.A. Little. 1973. Production, storage, and use of photosynthate during shoot elongation in balsam fir (*Abies balsamea*). Can. J. Bot. 51: 1161-1168.

Loehle, C. 1988. Tree life history strategies: the role of defenses. Can. J. For. Res. 18: 209-222.

Loehle, C. and G. Namkoong. 1987. Constraints on tree breeding: Growth tradeoffs, growth strategies, and defensive investments. For. Sci. 33: 1089-1097.

Lorio, P.L., Jr. 1986. Growth-differentiation balance: A basis for understanding southern pine beetle - tree interactions. For. Ecol. Mgmt. 14: 259-273.

Lorio, P.L., Jr. 1988. Growth differentiation-balance relationships in pines affect their resistance to bark beetles (Coleoptera: Scolytidae). p. 73-92. In: W.J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.) Mechanisms of Woody Plant Defenses Against Insects -- Search for Pattern. Springer-Verlag, New York.

Lowman, M.D. and J.D. Box. 1983. Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. Aust. J. Ecol. 8: 17-25.

MacLean, D.A. 1985. Effects of spruce budworm outbreaks on forest growth and yield. p. 148-175. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Matson, P.A., F.P. Hain and W. Mawby. 1987. Indices of tree susceptibility to bark beetles vary with silvicultural treatment in a loblolly pine plantation. For. Ecol. Mgmt. 22: 107-118.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119-161.

Mattson, W.J., R.A. Haack, R.K. Lawrence and S.S. Slocum. 1990. Considering the nutritional ecology of the spruce budworm in its management. For. Ecol. Mgmt., In Press.

Mattson, W.J. and C.N. Koller. 1983. Spruce budworm performance in relation to matching selected chemical traits of its hosts. p. 138-148. In: A.S. Isaev (ed.) The Role of Insect-Plant Relationship in the Population Dynamics of Forest Pests. Proc. Inter. Sympos., Irkutsk, U.S.S.R.

Mattson, W.J., N. Lorimer and R.A. Leary. 1982. Role of plant variability (trait vector dynamics and diversity) in plant/herbivore interactions. p. 295-303. In: H.M. Heybroek, B.R. Stephan and K. von Weissenberg (eds.) Resistance to Diseases and Pests in Forest Trees. Pudoc, Wageningen.

Mattson, W.J. and S.R. Palmer. 1988. Changes in levels of foliar minerals and phenolics in trembling aspen, *Populus tremuloides*, in response to artificial defoliation. p. 157-169. In: W.J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.) Mechanisms of Woody Plant Defenses Against Insects -- Search for Pattern. Springer-Verlag, New York.

Mattson, W.J. and J.M. Scriber. 1987. Nutritional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations. p. 105-146. In: F. Slansky Jr. and J.G. Rodriguez (eds.) Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York.

Mattson, W.J., G.A. Simmons and J.A. Witter. 1988. The spruce budworm in eastern North America. p. 309-330. In: A.A. Berryman (ed.) Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Press, New York.

Mattson, W.J., S.S. Slocum and C.N. Koller. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. p. 55-65. In: R.L. Talerico and M. Montgomery (eds.) Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. USDA For. Serv. Gen. Tech. Rept. NE-85.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. Can. Ent. 86: 439-454.

McIntyre, G.I. 1987. The role of water in the regulation of plant development. Can. J. Bot. 65: 1287-1298.

McKey, D. 1974. Adaptive patterns in alkaloid physiology. Amer. Nat. 108: 305-320.

McLaughlin, B.M. 1986. Performance of the spruce budworm, *Choristoneura fumiferana*, in relation to dietary and foliar levels of sugar and nitrogen. M.S. Thesis, Michigan State University, 86p.

McLean, J.A., P. Laks and T.L. Shore. 1983. Comparisons of elemental profiles of the western spruce budworm reared on three host foliages and artificial medium. p. 33-40. In: R.L. Talerico and M. Montgomery (eds.) Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. USDA For. Serv. Gen. Tech. Rept. NE-85.

McMorran, A.R. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Ent. 97: 58-62.

McNeill, S. and T.R.E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. p. 77-98. In: J.B. Harborne (ed.) Biochemical Aspects of Plant and Animal Coevolution. Acad. Press., London.

Miller, C.A. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool. 35: 1-13.

Miller, C.A., D.C. Eidt and G.A. McDougall. 1971. Predicting spruce budworm development. Canad. For. Serv. Bi-mo. Res. Notes 27: 33-34.

Mitchell, R.G., R.H. Waring and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. For. Sci. 29: 204-211.

Montgomery, M.E. and M.M. Czapowskyj. 1985. Nitrogen as an indicator of foliage quality to the spruce budworm. p. 494-495. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Mooney, H.A., S.L. Gulmon and N.D. Johnson. 1983. Physiological constraints on plant chemical defenses. p. 21-36. In: P.A. Hedin (ed.) Plant Resistance to Insects. Amer. Chem. Soc., Wash. D.C.

Morris, R.F. and C.A. Miller. 1954. The development of life tables for the spruce budworm. Can. J. Zool. 32: 283-301.

Morrison, D.F. 1976. Multivariate statistical methods. 2nd. ed. McGraw-Hill, New York, 415p.

Nienstaedt, H. 1963. The establishment of white spruce seed sources from the entire range of the species. USDA For. Serv., Unpublished Report.

Nienstaedt, H. 1969. White spruce seed source variation and adaptation to 14 planting sites in northeastern United States and Canada. Proc. 11th Meeting Comm. For. Tree Breeding in Canada, p. 183-194.

Nienstaedt, H. 1974. Genetic variations in some phenological characteristics of forest trees. p. 389-400. In: H. Lieth (ed.) Phenology and Seasonality Modeling. Springer-Verlag, New York.

Nienstaedt, H. 1985. Inheritance and correlations of frost injury, growth, flowering, and cone characteristics in white spruce, *Picea glauca* (Moench) Voss. Can. J. For. Res. 15: 498-504.

Nienstaedt, H. and H. Kang. 1987. Establishing a *Picea glauca* (Moench) Voss base breeding population for the Lake States region of the United States. Silvae Gen. 36: 21-30.

Nienstaedt, H. and J.P. King. 1970. Breeding for delayed budbreak in *Picea glauca* (Moench) Voss -- Potential frost avoidance and growth gains. Proc. FAO/IUFRO 2nd. World Consult. For. Tree Breeding, p. 61-80.

Nienstaedt, H. and A. Teich. 1972. The genetics of white spruce. USDA For. Serv. Res. Pap. WO-15, 24p.

Osawa, A., C.J. Spies and J.B. Dimond. 1986. Patterns of tree mortality during an uncontrolled spruce budworm outbreak in Baxter State Park, 1983. Maine Agric. Exper. Stn. Tech. Bull. 121, 69p.

Price, P.W. 1984. Insect ecology. 2nd. ed. John Wiley, New York, 607 p.

Rao, C.R. 1973. Linear statistical inference and its applications. 2nd. ed. John Wiley & Sons, New York, 625p.

Raske, A.G. 1985. Collapsing budworm populations. p. 141-142. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Raupp, M.J. 1985. Effects of leaf toughness on mandibular wear of the leaf beetle, *Plagiodera versicolora*. Ecol. Ent. 10: 73-79.

Raupp, M.J. and R.F. Denno. 1983. Leaf age as a predictor of herbivore distribution and abundance. p.91-124. In: R.F. Denno and M.S. McClure (eds.) Variable Plants and Herbivores in Natural and Managed Systems. Acad. Press, New York.

Rauter, R.M. 1985. Tree improvement policy guidelines for Ontario with special emphasis on white and black spruce. p. 193-202. In: D. Schmitt (ed.) Spruce-fir Management and Spruce Budworm. USDA For. Serv. Northeastern For. Exper. Stn., Gen. Tech. Rept. NE-99.

Redak, R.A. and R.G. Cates. 1984. Douglas-fir (*Pseudotsuga menziesii*)-spruce budworm (*Choristoneura occidentalis*) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. Oecologia 62: 61-67.

Regniere, J. 1987. Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Ent. 119: 717-728.

Retnakaran, A. 1983. Spectrophotometric determination of larval ingestion rates in the spruce budworm (Lepidoptera: Tortricidae). Can. Ent. 115: 31-40.

Roche, L. 1969. A genecological study of the genus *Picea* in British Columbia. New Phytol. 68: 505-554.

Rose, A.H. and J.R. Blais. 1954. A relation between April and May temperatures and spruce budworm larval emergence. Can. Ent. 86: 174-177.

Rossiter, M.C., J.C. Schultz and I.T. Baldwin. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. Ecology 69: 267-277.

SAS Institute Inc. 1988. SAS/STAT user's guide, Release 6.03 ed. SAS Institute Inc.; Cary, N.C. 1028p.

Schönherr, J. 1980. Dispersal of the European spruce budworm, *Choristoneura murinana* Hb. (Lepidoptera: Tortricidae). p. 128-133. In: A.A. Berryman and L. Safranyik (eds.) Proc. 2nd. IUFRO Conf. on Dispersal of Forest Insects: Evaluation, Theory and Management Implications.

Scriber, J.M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Oecologia 28: 269-287.

Scriber, J.M. 1978. The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: an ecological consideration. Ent. Exp. Appl. 24: 694-710.

Scriber, J.M. 1984a. Nitrogen nutrition of plants and insect invasion. p. 441-460. In: R.D. Hauck (ed.) Nitrogen in Crop Production. Amer. Soc. Agron., Madison, Wisconsin.

Scriber, J.M. 1984b. Host-plant suitability. p. 159-202. In: W.J. Bell and R.T. Carde (eds.) Chemical Ecology of Insects. Sinauer Assoc.; Sunderland, Mass.

Scriber, J.M. and F. Slansky Jr. 1981. The nutritional ecology of immature insects. Ann. Rev. Ent. 26: 183-211.

Shaw, G.G. and C.H.A. Little. 1973. Dispersal of second instar spruce budworm. Canad. For. Serv. Bi-mo. Res. Notes 29: 30-31.

Sheehan, K.A., W.P. Kemp, J.J. Colbert and N.L. Crookston. 1989. The western spruce budworm model: Structure and content. USDA For. Serv. Pacific Northwest Res. Stn., Gen. Tech. Rept. PNW-GTR-241, 70p.

Shepard, R.F. 1985. A theory on the effects of diverse host-climatic environments in British Columbia on the dynamics of western spruce budworm. p. 60-70. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Simmons, G.A., W. Cuff, B.A. Montgomery and J.M. Hardman. 1984. Projection Methods. p. 142-165. In: D.M. Schmitt, D.G. Grimble and J.L. Searcy (Tech. Coord.) Spruce Budworms Handbook - Managing the Spruce Budworm in Eastern North America. USDA For. Serv., Agr. Hdbk. 620.

Smith, K.G. 1981. Canonical correlation analysis and its use in wildlife habitat studies. p. 80-91. In: D.E. Capen (ed.) The Use of Multi-variate Statistics in Studies of Wildlife Habitat. USDA For. Serv. Gen. Tech. Rept. RM-87.

Strong, D.R., J.H. Lawton and R. Southwood. 1984. Insects on plants -- community patterns and mechanisms. Harvard Univ. Press, Cambridge, Mass. 313 p.

Sullivan, M.J. and C.A. Moncreiff. 1988. A multivariate analysis of diatom community structure and distribution in a Mississippi salt marsh. Bot. Marina 31: 93-99.

Thomas, A.W. 1976. Effects of temperature on emergence of second-instar spruce budworm larvae. Can. For. Serv., Maritimes For. Res. Ctr., Info. Rept. M-X-60, 8p.

Thomas, A.W. 1983. Foliage consumption by 6th-instar spruce budworm larvae, *Choristoneura fumiferana* (Clem.), feeding on balsam fir and white spruce. p. 47-48. In: R.L. Talerico and M. Montgomery (eds.) Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. USDA For. Serv. Gen. Tech. Rept. NE-85.

Thomas, A.W. 1987. The effect of age of current-year shoots of *Picea glauca* on survival, development time, and feeding efficiency of 6th-instar larvae of *Choristoneura fumiferana*. Ent. Exp. Appl. 43: 251-260.

Thomas, A.W. 1989. Food consumption and utilization by 6th-instar larvae of spruce budworm, *Choristoneura fumiferana*: a comparison on three *Picea* (spruce) species. Ent. Exp. Appl. 52: 205-214.

Thomson, A.J., R.F. Shepard, J.W.E. Harris and R.H. Silversides. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. Can. Ent. 116: 375-381.

Turgeon, J.J. 1986. The phenological relationship between the larval development of the spruce budmoth, *Zeiraphera canadensis* (Lepidoptera: Olethreutidae), and white spruce in northern New Brunswick. Can. Ent. 118: 345-350.

Vincent, J.F.V. 1982. The mechanical design of grass. J. Mater. Sci. 17: 856-860.

Volney, W.J.A. 1985. Comparative population biologies of North American spruce budworms. p. 71-84. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (eds.) Recent Advances in Spruce Budworms Research, Proc. CANUSA Spruce Budworms Res. Sympos.

Volney, W.J.A., W.E. Waters, R.P. Akers and A.M. Liebhold. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Ent. 115: 199-209.

von Rudloff, E. 1972. Seasonal variation in the composition of the volatile oil of the leaves, buds, and twigs of white spruce (*Picea glauca*). Can. J. Bot. 50: 1595-1603.

von Rudloff, E. 1975a. Seasonal variation in the terpenes of the foliage of black spruce. Phytochem. 14: 1695-1699.

von Rudloff, E. 1975b. Seasonal variation of the terpenes of the leaves, buds, and twigs of blue spruce (*Picea pungens*). Can. J. Bot. 53: 2978-2982.

von Rudloff, E. and M. Granat. 1982. Seasonal variation of the terpenes of the leaves, buds, and twigs of balsam fir (*Abies balsamea*). Can. J. Bot. 60: 2682-2685.

von Schönborn, A. 1966. The breeding of insect-resistant forest trees in central and northwestern Europe. p. 25-27. In: H.D. Gerhold, R.E. McDermott, E.J. Schreiner and J.A. Winieski (eds.) Breeding Pest-Resistant Trees. Pergamon Press, London.

Wagner, M.R. and E.A. Blake. 1983. Western spruce budworm consumption -- Effects of host species and foliage chemistry. p. 49-54. In: R.L. Talerico and M. Montgomery (eds.) Forest Defoliator -- Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. USDA For. Serv. Gen. Tech. Rept. NE-85.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90-105.

Whitham, T.G. 1981. Individual trees as heterogeneous environments: Adaptation to herbivory or epigenetic noise? p.9-27. In: R.F. Denno and H. Dingle (eds.) Insect Life History Patterns -- Habitat and Geographic Variation. Springer-Verlag, New York.

Whitham, T.G. 1983. Host manipulation of parasites: Within-plant variation as a defense against rapidly evolving pests. p.15-41. In: R.F. Denno and M.S. McClure (eds.) Variable Plants and Herbivores in Natural and Managed Systems. Acad. Press, New York.

Wickman, B.E. 1976. Phenology of white fir and Douglas-fir tussock moth egg hatch and larval development in California. Environ. Ent. 5: 316-322.

Wilkinson, R.C. 1977a. Inheritance of budbreak and correlation with early height growth in white spruce (*Picea glauca*) from New England. USDA For. Serv. Res. Pap. NE-391.

Wilkinson, R.C. 1977b. Height growth performance of white spruce (*Picea glauca* (Moench) Voss) provenances in central Maine. Proc. Northeast. For. Tree Improv. Conf. 25: 87-93.

Wilkinson, R.C., J.W. Hanover, J.W. Wright and R.H. Flake. 1971. Genetic variation in the monoterpene composition of white spruce. For. Sci. 17: 83-90.

Winer, B.J. 1971. Statistical principles in experimental design. 2nd. ed. McGraw-Hill, New York, 907p.

Witter, J.A. and L.A. Waisanen. 1978. The effect of differential flushing times among trembling aspen clones on tortricid caterpillar populations. Environ. Ent. 7: 139-143.

Wright, J.W., H. Nienstaedt, W.A. Lemmien, J.N.Bright, M.W. Day and R.L. Sajdak. 1977. Better white spruce for Michigan. Michigan State Univ. Agric. Exper. Stn. Res. Rept. 316, 8p.