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PERFORMANCE OF THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA*, IN RELATION TO DIETARY AND FOLIAR LEVELS OF SUGAR AND NITROGEN

By

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ABSTRACT

PERFORMANCE OF THE SPRUCE BUDWORM,
CHORISTONEURA FUMIFERANA, IN RELATION TO DIETARY
AND FOLIAR LEVELS OF SUGAR AND NITROGEN

By

Brian Matthew McLaughlin

The effect of different sugar/nitrogen ratios on spruce budworm (*Choristoneura fumiferana*) performance was measured by manipulating these two nutrients in artificial diets, and by evaluating their performance on host trees (balsam fir and white and black spruce) that differed in their soluble sugar/nitrogen ratios. The optimal combination of sugar (6 levels) and nitrogen (4 levels) in artificial diets for all measured budworm performance variables was 12.8% sugar and 4.9% nitrogen. This combination had a sugar/nitrogen ratio of 2.61/1. This optimal ratio increased in low-level nitrogen diets.

Balsam fir and white spruce were equally suitable host plants for most study areas. Foliar nitrogen and sugar levels varied considerably within tree species throughout the life cycle of the budworm. There were no consistent correlations between budworm performance and nitrogen or sugar from year to year. There were, however, some consistant correlations within single years for both tree species.

To my grandfather and grandmother,

James and L. Mary McTigue

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GENERAL INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), was first described in 1865 by Clemens (Freeman 1958). Since 1865 the scientific name of the spruce budworm has changed many times, receiving seven different names under five different genera (Bakuzis and Hanson 1965). Its present name, *Choristoneura fumiferana*, was proposed by Freeman in 1947. The last taxonomic change to affect the budworm occurred in 1953 when Freeman distinguished between two forms of the spruce budworm: *Choristoneura fumiferana*, the spruce budworm and *Choristoneura pinus*, the jack pine budworm (Bakuzis and Hanson 1965).

The genus *Choristoneura* in North America is composed of 18 species, five of which are spruce and fir feeders while the remaining thirteen forage primarily on pines and a variety of deciduous trees (Freeman 1958 and 1967, Powell 1964). The family Tortricidae is one of the largest families of the Microlepidoptera with about 950 North American species (Borror et al. 1981). In addition to the spruce budworm there are many other economically important species in the family Tortricidae. Examples are the codling moth, *Cydia pomenella* (L.) which is an important pest of apples and other fruits, and the oriental fruit moth,*Grapholitha molesta* (Busck) which is an oriental species that is widely distributed in the United States and an important pest of peaches and other fruits. The western spruce budworm, *Choristoneura occidentalis* (Freeman), is a close relative of the eastern spruce budworm and is an important pest of Douglas fir, *Pseudotsuga menziesii* (Mirb) Franco, white fir, *Abies concolor* (Gord. and Glend.) Hoopes, and Englemann spruce, *Picea engelmanni*(Parry), in the western United States.

The range of the eastern spruce budworm in North America follows the occurrence and distribution of its two major host plants, balsam fir, *Abies balsamea* (L.) Mill, and white spruce, *Picea glauca* (Moench) Voss, and extends from Maine and New Brunswick in eastern North America to Minnesota and Manitoba in midwestern North America (Montgomery et al. 1982). The states most affected by the spruce budworm are Maine, New Hampshire, New York, Michigan, Wisconsin and Minnesota (Kucera and Orr 1981). The spruce budworm has a one year life cycle with the larval period beginning in late July or early August. Newly hatched larvae seek protected locations on the host plant where they molt to second instars and then enter diapause in preparation for the onset of winter. In early spring (late April-early May) these second instar larvae emerge and mine 1-year-old needles or buds. When current year buds begin to swell and expand, larvae in needle mines migrate to this new food source and there complete their larval development in about four weeks (McGugan 1954). After about one week in the pupal stage, moths emerge in early July and live from four to six days, consuming water only and ovipositing on the foliage of selected host trees. Städler (1974) found that acceptance of oviposition sites by female budworm was influenced by the shape and chemical composition (alpha- and beta-pinene) of the host plant substrate. Larvae hatch from eggs within one week after oviposition and begin the entire cycle again.

Spruce budworm outbreaks occur periodically (every 40 to 70 years) and usually appear to originate in small areas from which they spread rapidly and cover extensive regions (Swaine et al. 1924, Graham and Orr 1940). Outbreaks that are not controlled can last eight to ten years and terminate when food supplies become scarce and tree mortality is high (Hudak and Raske 1981). Balsam fir is the most vulnerable host plant and usually dies after four to five consecutive years of severe defoliation of current year foliage (Hudak and Raske 1981). White spruce and red spruce, Picea rubens (Sarg.), are less vulnerable because they can usually withstand defoliation for six or more consecutive years before dying (Hudak and Raske 1981).

In areas where forests are valuable resources to local economies, spruce budworm outbreaks can be devastating. Uncontrolled outbreaks can cause economic losses ammounting to millions of dollars in forest-dependent economies (Sterner and Davidson 1981). Control of spruce budworm populations has traditionally been accomplished through the aerial application of insecticides. Such programs for budworm control are unique in entomology because they are the largest and most specialized pest control programs in the world (Montgomery et al 1983). DDT was the first pesticide used on the budworm, being applied in the late 1950's and early 1960's. Since the decline of chlorinated hydrocarbon use in the 1960's and because of the high financial and social costs of modern day chemical spray programs, forest entomologists have tried to take a more integrated approach to budworm control. Today, large scale spray programs are still the most effective means of controlling budworm outbreaks. However, the use of natural enemies such as the parasitic wasps Trichogramma minutum (Riley) and Brachymeria intermedia (Nees); microbial insecticides such as Bacillus thuringiensis toxin; and insect growth regulating compounds may be combined with silvicultural practices and conventional spray programs to control budworm populations (Montgomery et al. 1983).

The spruce budworm has been studied for over 70 years. Until recently, the focus of this intensive research has been centered on either its general biology and its population dynamics or its impact upon the forest systems that it inhabits. Forests systems supporting budworms have traditionally been classified according to their physical characteristics such as slope, soil type, species composition, stand density and tree age. These characteristics affect the growth and development of the host trees and ultimately affect the growth and development of spruce budworm populations. More recently, scientists have focused on the finer details of insect/host plant interactions to better understand the growth and behavior of the spruce budworm. For example, the nutritional quality of a host plant is directly determined by the quality and quantity of chemicals in it's tissues that can be utilized as food. Among the principal nutrients in spruce budworm host plants are soluble carbohydrates (sugar) and proteins (nitrogen).

In the following pages, I have explored the response (performance) of spruce budworm to varying levels and ratios of soluble carbohydrates and nitrogen in artificial diets. I have also determined the foliar sugar and nitrogen content of selected host plants and correlated these findings with spruce budworm performance on these same trees.

INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is an outbreak insect folivore that feeds primarily on the current growth of balsam fir, *Abies balsamea*, white spruce, *Picea glauca* and red spruce, *Picea rubens*, in North America. Mechanisms underlying the development and collapse of its outbreaks are still largely unknown. However, variations in the nutritional quality of host plants are suspect (Mattson et al. 1983, Fleming 1983). Among the principal plant nutrients required by insects are soluble carbohydrates and proteins. Little (1970) reported that fructose, glucose, sucrose, raffinose and starch were the predominant carbohydrates in current and one-year old needle growth of balsam fir. Similar findings were reported by Chalupa and Fraser (1968) for white spruce. Levels of total soluble sugars vary greatly during the growing season (Little 1970) as well as from year to year (Shaw and Little 1976). Little (1970) also found seasonal variations in the total starch content of developing shoots of balsam fir.

Harvey (1974) tested these carbohydrates as well as others such as maltose and sorbitol for their nutritional quality in spruce budworm diet. He found that all were basically acceptable except for starch. Harvey (1974) also found that an absolute requirement for sugar could not be demonstrated but nevertheless observed an increase in female adult weight with increasing levels of sucrose. Both Harvey (1975) and Shaw (1973) concluded that most starches were nutritionally poor substitutes for sucrose in artificial diets.

Soluble sugars are not only important as energy sources but also as feeding stimulants. Heron (1965) and Albert and Jerret (1980) found sugars to be among the most important host plant chemicals to stimulate spruce budworm feeding. Albert et al. (1982) further showed that budworm feeding behavior is most strongly responsive to sucrose, followed by fructose, inositol and glucose. Albert et al. (1982) concluded that the behavioral feeding threshold for sucrose is between 10-4 and 10-3 M, with the optimal feeding response occurring between 0.01 to 0.05 M sucrose.

Less exacting studies have been done on the importance of plant protein on spruce budworm growth and development. Shaw and Little (1972, 1976) showed a rapid seasonal decline in foliar nitrogen in current year needles of balsam fir. Mattson et al. (1983) established a similar seasonal decay in foliar nitrogen, for both balsam fir and white spruce. Mattson et al. (1983) further demonstrated that tree to tree variations in spruce budworm growth were consistently positively correlated to foliar nitrogen. Shaw et al. (1978) and Mattson et al. (1983) increased foliar nitrogen levels in balsam fir through fertilization and found that in response, budworm pupal weights increased. Brewer et al. (1985) fertilized white fir seedlings at five different nitrogen levels and found that pupal weight gains for the western spruce budworm, Choristoneura occidentalis (Freeman) increased up to a nitrogen level of 2.41%, after which they declined. McMorran (1965) synthesized an artificial diet for the spruce budworm which contained about 4.9% nitrogen on a dry weight basis and found that female larvae reared on this diet attained an average pupal fresh weight of 121.7 mg with a range of 93.5 to 154.0 mg. Harvey (1974) measured budworm performance on diets containing about 6.34% nitrogen and little if any soluble sugars and found low pupal weights, protracted development and poor survival, although some surviving females were able to lay viable eggs.

More recently, nutritional studies have focused on the balance between soluble carbohydrates and protein (nitrogen) and how varying the ratios of these two nutrients affects insect growth. For example, Tsiropoulos (1981) found that reproduction by the olive fruit fly, Dacus oleae (Gmelin), was best under a carbohydrate/nitrogen ratio of 25/1, where higher nitrogen contents reduced egg deposition. Waldbaur et al. (1984) found that last instar larvae of the corn earworm, Heliothis zea (Boddie), preferred and performed best at a 1.56/1 carbohydrate/nitrogen ratio. Manipulation of soluble carbohydrate/nitrogen ratios was done indirectly by Shaw et al. (1978) for spruce budworm when they fertilized young balsam fir trees. Fertilized trees had both higher total nitrogen and total sugars and a higher carbohydrate/nitrogen ratio than controls (5/1 vs 2/1). Spruce budworm larvae reared on foliage of fertilized trees had higher survival rates and higher pupal and adult weights than those reared on unfertilized trees. Harvey (1974) manipulated artificial diets to obtain soluble carbohydrate/nitrogen ratios ranging from 1.1/1 to 8.82/1 and found that higher ratios produced larger female pupae than lower ratios.

The purpose of this study was to further define the influence of soluble carbohydrate/nitrogen ratios on spruce budworm performance by manipulating these two major nutrients in artificial diets, and by evaluating budworm performance on balsam fir and white spruce trees which differed in their soluble carbohydrate/nitrogen ratios.

Methods and Materials

Insects were obtained as diapausing second instar larvae from the rearing facility of the Forest Pest Management Institute, Canadian Forest Service, at Sault Ste. Marie, Canada. Larvae were reared on a meridic artificial diet following the procedures of McMorran (1965). Four larva were transferred to individual 1-oz tranlucent plastic creamer cups, capped with paper lids and then reared until adult eclosion at $22^{0}C \pm 1^{0}$, ca. 50% RH, and a 16:8 L:D photoperiod. Each treatment consisted of 50 creamer cups totaling 200 insects per treatment. During early larval instars creamer cups were examined every other day for budworm progress. During later larval instars creamer cups were checked daily and all pupae were removed and weighed within 24 hours of pupation. Pupae were placed separately into vials, returned to the incubator and allowed to complete metamorphasis. Adults were frozen within 24 hours after eclosion and dried at 75 ^{o}C for 24 hours before final weighing.

To obtain nitrogen and carbohydrate levels other than those in the standard McMorran (1965) diet, the levels of sucrose, casein, wheat germ and cellulose (all from ICN Nutritional Biochemicals, Clevland, Ohio) were manipulated. All other ingredients were kept constant. All diets contained a constant dry weight by manipulation of these variables. Wheat germ contains approximately 16.2% soluble sugars (Fraser and Holmes 1957), which was accounted for in calculations of % dry weight sugar in diets. Wheat germ and casein were used as nitrogen sources with wheat germ containing 6% nitrogen (Fraser and Holmes 1957) and casein 14% (ICN Nutritional Biochemicals; personal communication) nitrogen by dry weight. Commercial brand alphacel (cellulose) was found to contain 0.6% nitrogen (Kjeldahl procedure; Mattson unpublished data), which was considered unavailable because of the budworm's inability to hydrolyze cellulose. The standard McMorran (1965) diet contains about 4.9% nitrogen of which casein makes up 74% and wheat germ 26%. This casein/wheat germ ratio was kept constant at all nitrogen levels to avoid changing the balance of amino acids in the diet.

A matrix design employing four nitrogen levels and six sugar levels was used. Nitrogen levels were 1.5, 2.68, 5.36 and 7.0 grams or 1.38, 2.45, 4.90 and 6.41 on a % dry weight basis. Sugar levels were 3.88, 7.0, 14.0, 21.0, 28.0, and 42.0 grams or 3.55, 6.41, 12.80, 19.23, 25.64, and 38.46 on a % dry weight basis. Sugar/nitrogen ratios were calculated on a gram/gram dry weight basis. Diets containing 4.9 grams nitrogen and above were terminated at 40 days from experiment initiation. Diets containing nitrogen levels below 4.90 grams nitrogen were terminated at 50 days due to protracted development. I used a two way analysis of variance to measure the main effects of nitrogen and sugar levels on budworm performance. Insect performance was measured using the following variables; fresh weight (fwt) of pupae, dry weight (dwt) of adults, pupal and adult growth rates (fwt of pupae or dwt of adult/days to develop) developmental rate (100/days to develop) for pupal and adult stages and survival of larvae to adult eclosion. Because weight of female budworm pupae has been shown to be directly related to adult fecundity (Miller 1957), pupal weight was used to estimate fecundity in this study.

Oils were added to diet media via an acetone solvent when diets contained added fatty acids. This oil/acetone solution was applied to the casein portion of the diet and allowed to evaporate completely before mixing.

Insect frass from diets was collected and dried for 24 hours at 75 ^{o}C for soluble carbohydrate analysis. Frass samples were extracted in quantities of 125 mg with 25 ml of 100% methanol on a shaker for 24 hours. Samples were then centrifuged and 10 ml of the centrifuged extract was placed in a sample concentrator and allowed to dry completely. Samples were then reconstituted with 2 ml of an 80/20 mixture of acetonitrile/water and filtered through C18 Sep Pac cartridges (Waters Associates, Milford, Massachusetts) and millipore prefilters (Waters Associates, Milford, Massachusetts). A 75 ul sample of the concentrated extract was then injected into an HPLC equipted with a Waters carbohydrate analysis column (Waters Associates, Milford, Massachusetts). Operating conditions for HPLC soluble carbohydrate analysis followed the general procedure outlined in AOAC (1980 methods No. 31). Flow rate was 2 ml/min and eluting solvent used was acetonitrile/water (80/20). An external standard, a refractive index detector and a Hewlett Packard integrator were used to quantify the three major sugars (fructose, glucose and sucrose) found in budworm frass.

Field experiments were conducted at separate sites near International Falls (Minnesota), Antigo (Wisconsin) and Wellston and Augusta (Michigan). Diapausing second instar diapausing larvae were obtained as mentioned before from the Canadian Forest Pest Management Institute, Canadian Forest Service in Sault Ste Marie, Ontario. Four groups (25 larvae per group) were placed on mid-crown branches in early spring on each of 20 to 50 trees per site. Each group of insects were securely enclosed within fine-mesh, translucent cloth sleeve cages that were ca. 75-cm long. Insects were allowed to develop until most had pupated in the field. Branches were then removed from the trees and returned to the lab for processing. Pupae were allowed to complete metamorphosis in the lab at which point the newly emerged adults were frozen, oven dried for 24 hours at 75 ^{o}C and weighed immediatly. Foliage samples from other branches on experimental trees were collected when larvae were in the fifth and sixth developmental stages. Samples were put on ice in the field, brought back to the laboratory and immediately frozen. Samples were freeze-dried at a later date, cleaned and ground to a fine powder with a micromill. Foliage samples were processed and analyzed for the major soluble carbohydrates in balsam fir and white spruce (fructose, glucose and sucrose) using the same procedures previously outlined for frass carbohydrate analysis. Nitrogen analysis were conducted by Mr. Bruce A. Birr (Technician, USFS, Michigan State University) using the Kjeldahl procedure. For more details concerning field experiment methods, please see Mattson et al 1983.

RESULTS

Diet Matrix Study

The performance of male and female insects followed similar patterns among all diet treatments. Hence to avoid unnecessary discussion, only female growth patterns will be discussed for all parameters except survival. Data for both sexes, however, are presented in the tables and figures.

Combined Female and Male Larval Survival to Adult Eclosion

Survival on diets containing 1.38% nitrogen was extremely poor at all sugar levels ranging from a minimum of 0.5% (38.46% sugar) to a maximum of 5.8% (19.23% sugar), (Table 1 and Figure 1). Survival on diets containing twice as much nitrogen (2.45%) increased about 10-fold, ranging from a low of 24.5% (38.46% sugar) to a high of 52.2% (12.80% sugar). Survival on diets containing 4.90% nitrogen was even higher, ranging from 44.5% (19.23% sugar) to 72.0% (12.80% sugar). The latter was, in fact, the highest mean urvival for any sugar/nitrogen combination. At the highest nitrogen level (6.41%), survival no longer increased and was relatively uniform across all sugar levels ranging from 52.0% (3.55% sugar) to 59.0% (19.23% sugar).

Table 1. Percent larval survival to adult eclosion. n=number of experiments per treatment; 200 insects per experiment. Diets at levels where blanks (----) occur in tables 1-13 could not be formulated with standard ingredients.

	Nitrogen % Dry Weight				
Sugar % dw	1.38	2.45	4.90	6.41	Grand Mean
3.55	2.5 n=2	28.0 n=2	54.0 n=4	52.0 n=2	34.1
6.41	4.5 n=2	41.5 n=3	45.5 n=4	54.0 n=2	36.4
12.80	4.5 n=2	52.2 n=3	72.0 n=5	55.2 n=2	46.0
19.23	5.8 n=2	39.0 n=2	44.5 n=2	59.0 n=2	37.1
25.64	2.5 n=2	31.8 n=3	56.7 n=10	----	30.3
38.46	0.5 n=2	24.5 n=2	----	----	12.5
Grand Mean	3.4	36.2	54.5	55.1	

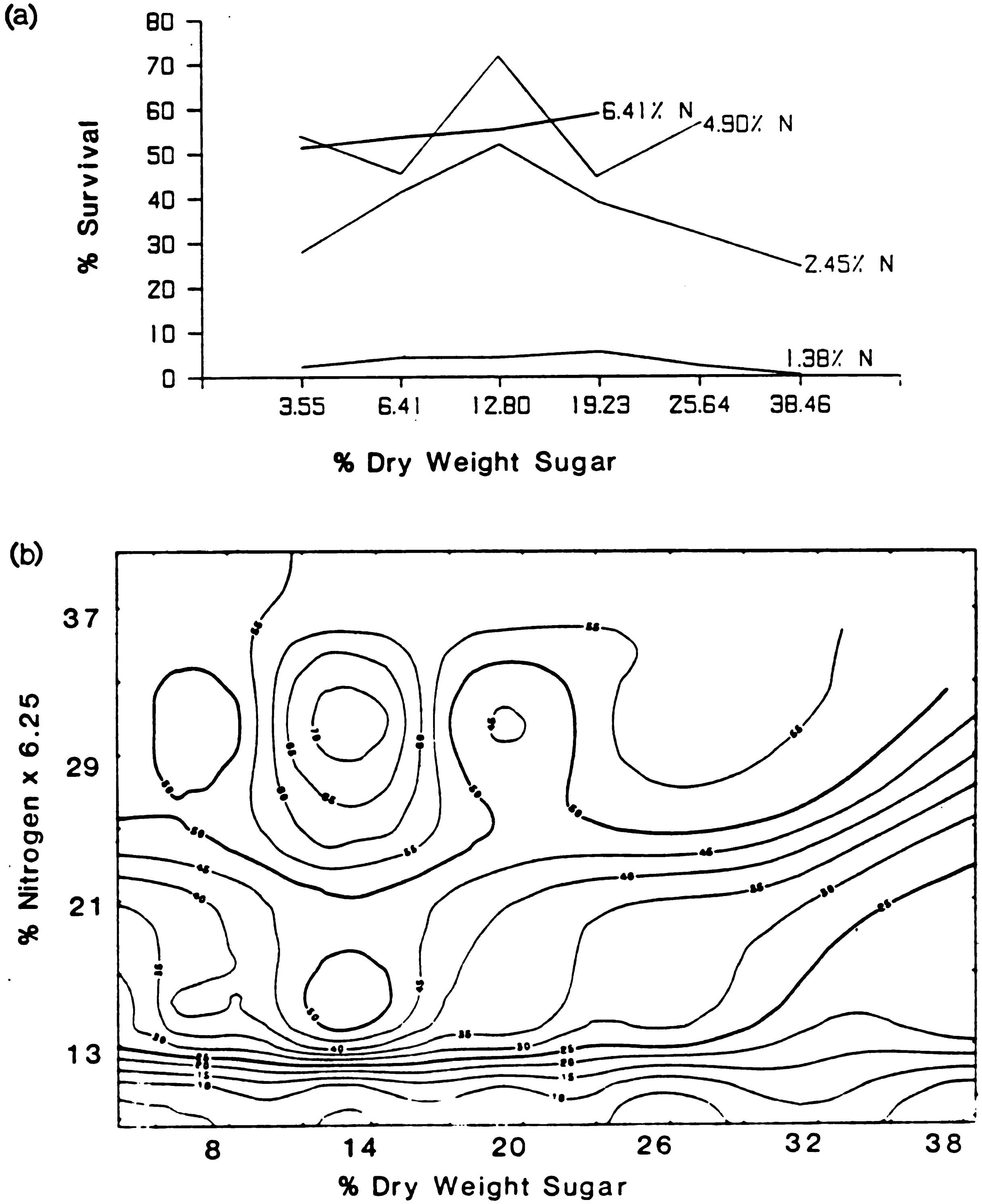


Figure 1. Combined male and female larval survival to the pupal stage (%) in relationship to dietary levels of sugars and nitrogen (% dw).

Pupal Weight

Female pupal weights were clearly dependent on both dietary nitrogen and sugar levels. Pupal weight was significantly lower at the 1.38% nitrogen level than at all other higher nitrogen levels (Tables 2,3 and Figures 2,3). On the lowest nitrogen diets, weights ranged from 66.7 mg (38.46% sugar) to 84.4 mg (19.23% sugar). On diets containing twice as much nitrogen (2.45%), weights increased about 30%, ranging from 87.8 mg (3.55% sugar) to 108.2 mg (19.23 % sugar). At the next highest nitrogen level (4.90%) weights were only about 10% higher, ranging from 98.8 mg (3.55% sugar) to 114.1 mg (6.41 and 12.80% sugar). The latter (114.1 mg) was the highest mean female pupal fresh weight for any sugar/nitrogen combination. At the highest nitrogen level (6.41%), weights declined slightly, ranging from a low of 99.9 mg (6.41% sugar) to a high of 107.0 mg (12.80% sugar).

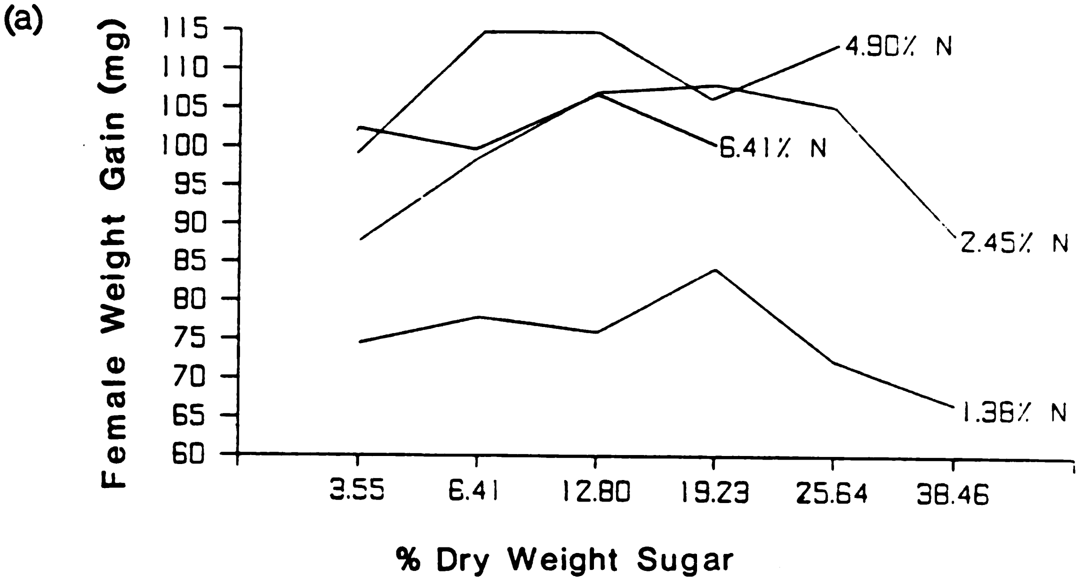
Adult Weight

Female adult weight, as was true for pupal weight, was clearly dependent on both dietary sugar and nitrogen levels (Tables 4,5 and Figures 4,5). Adult weights were again lower at 1.38% nitrogen than at all other higher nitrogen levels. On these diets, weights ranged from 12.5 mg (3.55% sugar) to 16.0 mg (19.23% sugar). On diets containing twice as much

Table 2. Female pupal fresh weight (mg) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	74.6±4.1 n=4 (c,1)*	87.8±4.0 n=34 (b,c,4)	98.8±1.8 n=162 (a,b,3)	102.2±2.6 n=91 (a,1)	98.2 (3)
6.41	78.0±4.1 n=8 (c,1)	98.6±3.1 n=57 (b,2,3)	114.1±2.2 n=128 (a,1)	99.9±2.4 n=104 (b,1)	105.2 (2)
12.80	75.9±4.7 n=13 (c,1)	107.0±2.1 n=91 (b,1)	114.1±1.4 n=202 (a,1)	107.0±2.7 n=102 (b,1)	109.5 (1)
19.23	84.4±4.6 n=11 (b,1)	108.2±3.2 n=64 (a,1)	106.2±2.4 n=99 (a,2)	100.5±2.5 n=109 (a,1)	103.6 (2)
25.64	72.3±2.5 n=4 (c,1)	105.2±2.9 n=53 (b,1,2)	113.7±1.1 n=422 (a,1)	------	112.4 (1)
38.46	66.7±13.6 n=2 (b,1)	88.7±4.1 n=30 (a,3,4)	------	------	87.3 (3)
Grand Mean	77.6 (d)	101.8 (c)	110.7 (a)	102.3 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).



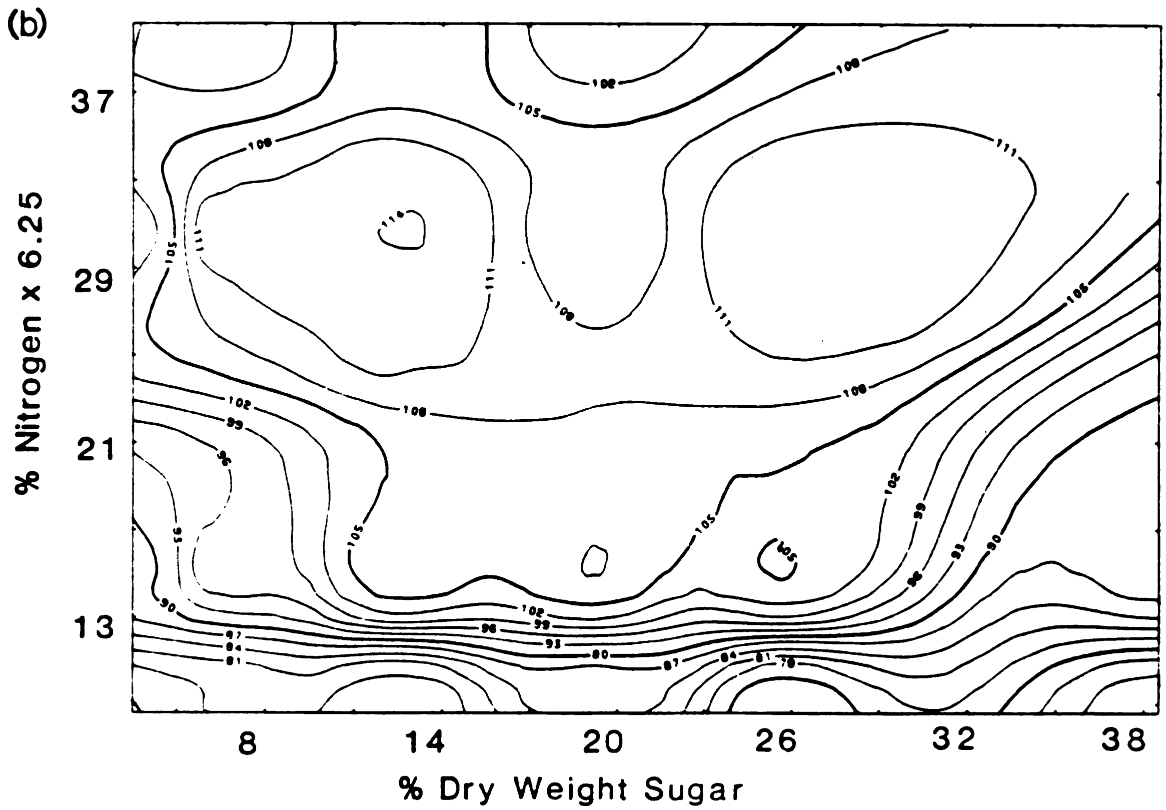


Figure 2. Female pupal fresh weight (mg) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 3. Male pupal fresh weight (mg) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	43.3±3.9 n=6 (c,1,2)*	63.0±1.9 n=56 (b,2)	68.4±1.0 n=183 (a,4)	67.6±1.4 n=104 (a,1)	66.8 (3,4)
6.41	46.7±2.5 n=18 (c,1,2)	67.0±1.9 n=87 (b,1,2)	74.8±1.2 n=171 (a,2)	66.3±1.6 n=126 (b,1)	69.2 (2,3)
12.80	52.4±3.7 n=18 (c,1)	70.6±1.2 n=140 (b,1)	78.1±1.0 n=296 (a,1)	69.0±1.4 n=122 (b,1)	73.5 (1)
19.23	50.1±1.9 n=31 (b,1)	65.5±1.8 n=79 (a,2)	66.3±1.5 n=99 (a,4)	68.3±1.6 n=157 (a,1)	65.6 (4)
25.64	43.8±3.4 n=14 (c,1,2)	67.2±1.4 n=85 (b,1,2)	71.8±0.8 n=542 (a,3)	------	70.5 (2)
38.46	36.5±5.8 n=6 (b,2)	48.5±2.2 n=42 (a,3)	------	------	47.0 (5)
Grand Mean	47.6 (d)	65.8 (c)	72.7 (a)	67.8 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

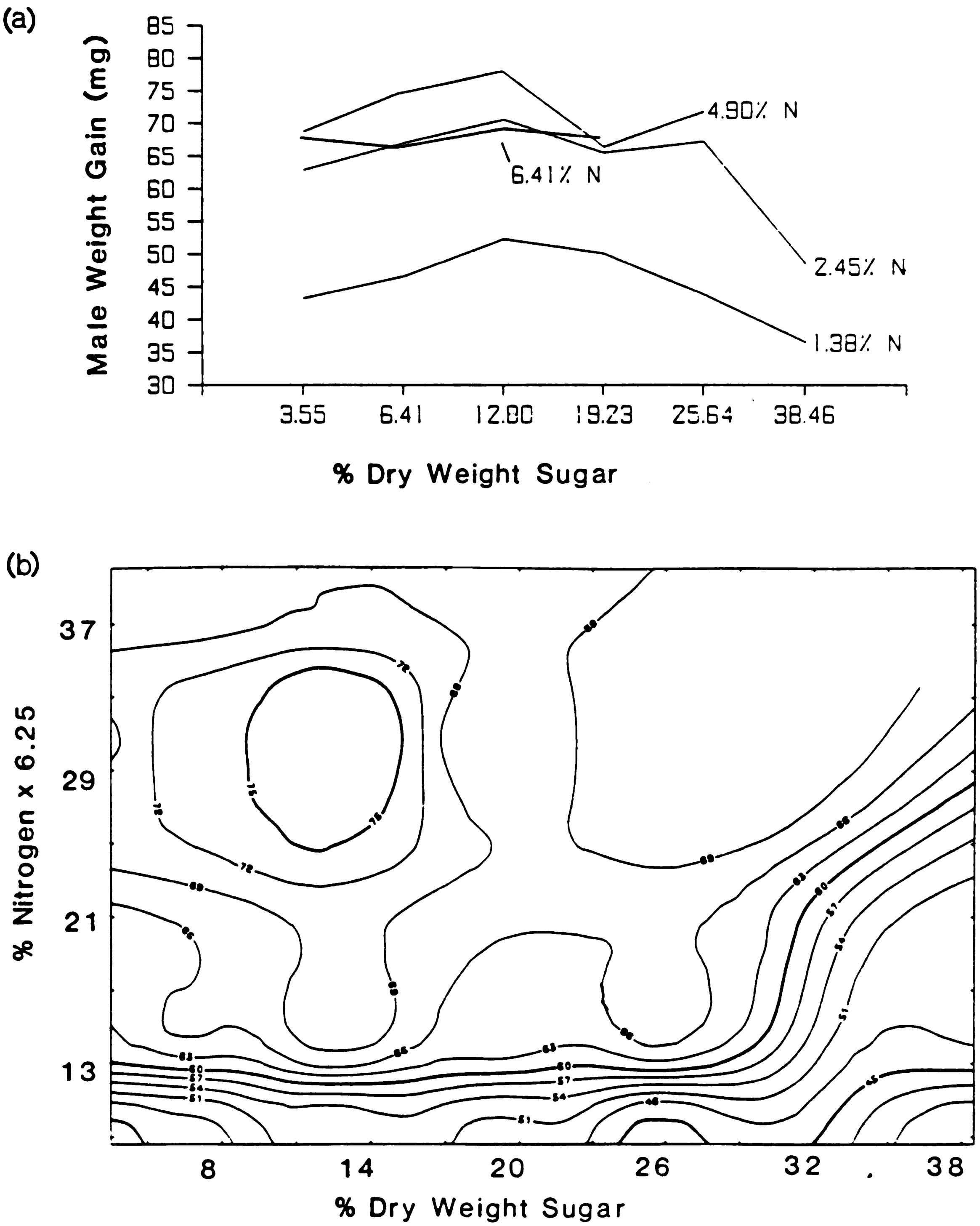


Figure 3. Male pupal fresh weight (mg) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 4. Female adult weight (mg) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	12.5±1.2 n=4 (d,2)*	14.7±1.1 n=22 (c,d,3)	17.4±0.6 n=62 (b,d,3)	19.9±0.6 n=78 (a,1)	18.1 (5)
6.41	12.6±1.9 n=5 (b,2)	18.6±0.6 n=79 (a,2)	20.0±0.5 n=111 (a,2)	19.8±0.6 n=95 (a,1)	19.4 (4)
12.80	15.3±1.4 n=9 (c,2)	20.7±0.5 n=96 (b,1)	23.8±0.5 n=131 (a,1)	21.1±0.6 n=85 (b,1)	21.9 (2)
19.23	16.0±1.1 n=10 (b,2)	21.1±0.8 n=54 (a,1)	21.3±0.6 n=89 (a,2)	20.3±0.6 n=89 (a,1)	20.7 (3)
25.64	12.7±1.1 n=4 (c,2)	20.8±0.7 n=67 (b,1)	23.5±0.3 n=358 (a,1)	------	22.9 (1)
38.46	16.1±0.0 n=1 (b,1)	17.0±1.0 n=26 (a,2,3)	------	------	17.0 (5)
Grand Mean	14.5 (c)	19.6 (b)	22.3 (a)	20.2 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

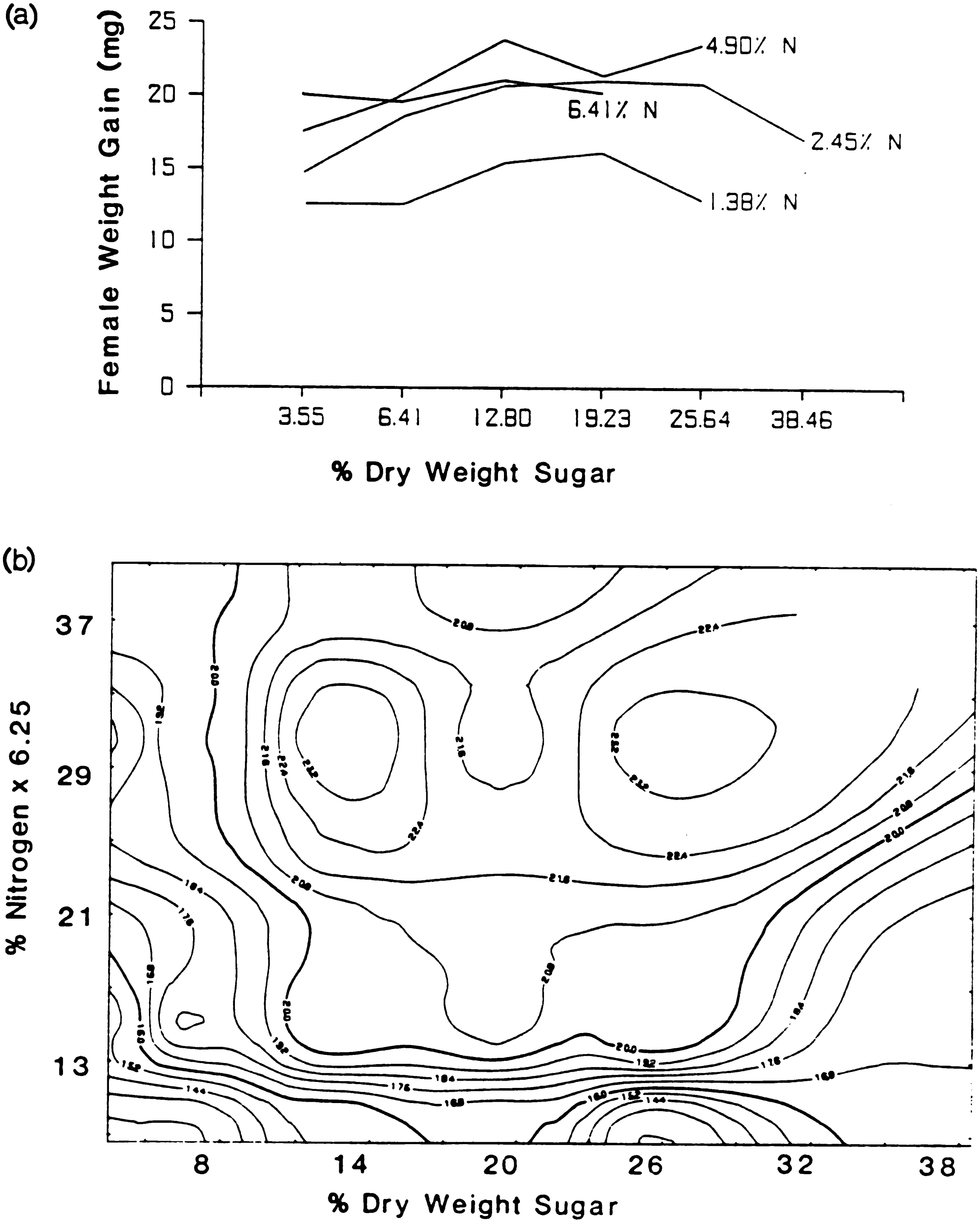


Figure 4. Female adult dry weight (mg) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 5. Male adult weight (mg) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	5.2±0.5 n=6 (c,3)*	8.2±0.3 n=34 (b,2)	8.7±0.3 n=43 (b,4)	10.0±0.2 n=90 (a,1)	9.1 (3)
6.41	7.7±0.4 n=13 (b,2)	8.9±0.3 n=87 (b,2)	10.1±0.2 n=160 (a,3)	9.8±0.2 n=104 (a,1)	9.6 (2,3)
12.80	8.8±1.1 n=9 (b,2)	10.1±0.3 n=117 (b,1)	11.4±0.2 n=125 (a,1)	10.5±0.3 n=98 (b,1)	10.7 (1)
19.23	7.5±0.4 n=13 (b,2)	9.9±0.3 n=69 (a,1)	10.1±0.3 n=89 (a,3)	10.2±0.3 n=121 (a,1)	10.0 (2)
25.64	5.6±0.8 n=6 (b,3)	10.5±0.3 n=68 (a,1)	10.9±0.1 n=472 (a,2)	------	10.8 (1)
38.46	8.0±0.0 n=1 (a,1)	7.9±0.4 n=28 (a,2)	------	------	7.9 (4)
Grand Mean	7.3 (d)	9.6 (c)	10.6 (a)	10.1 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p <$ 0.05 level (Ducans multiple range test).

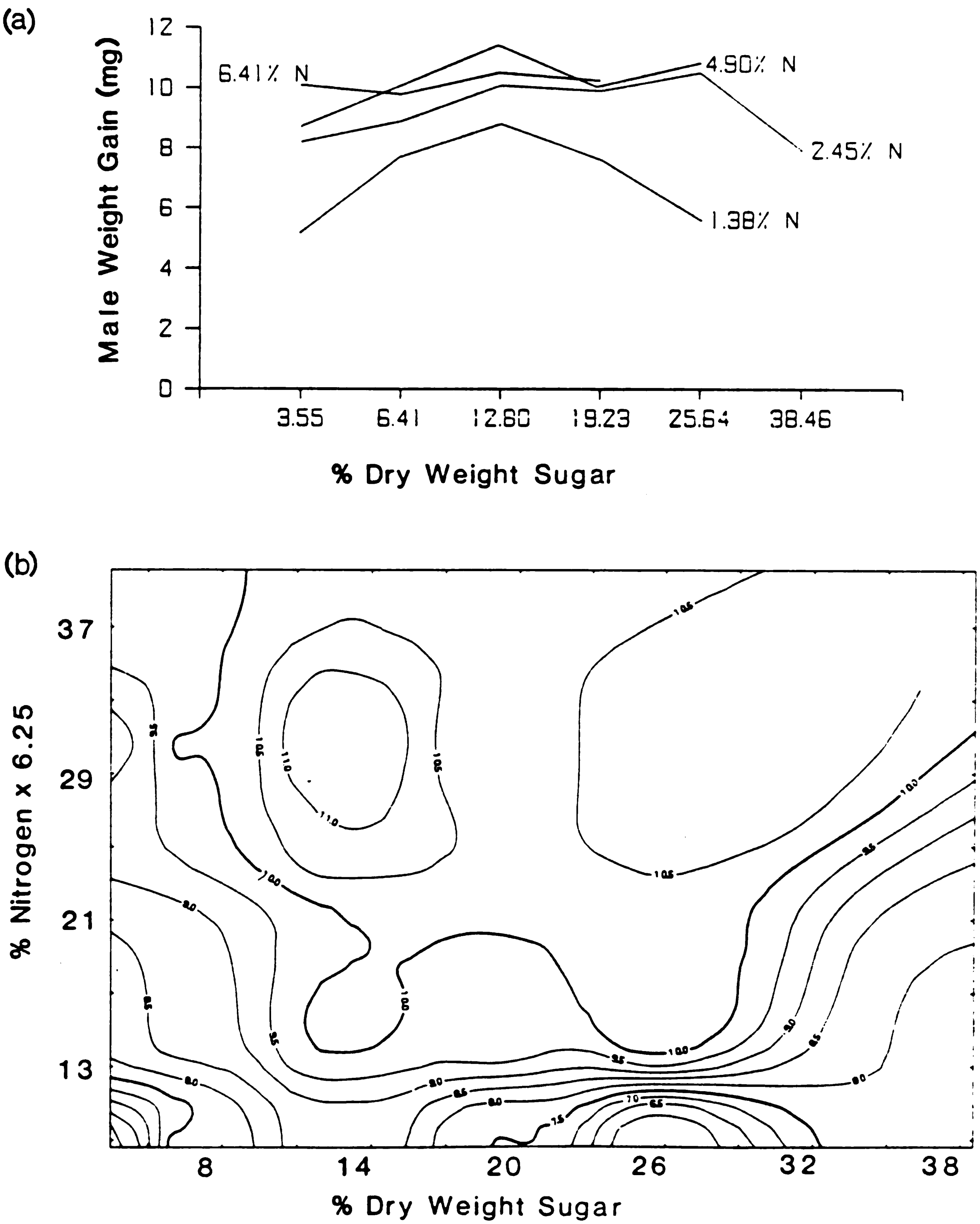


Figure 5. Male adult dry weight (mg) in relationship to dietary levels of sugars and nitrogen (% dw).

nitrogen (2.45%), mean weights increased about 35%, ranging from a low of 14.7 mg (3.55% sugar) to a high of 21.1 mg (19.23% sugar). Adult weights were still higher at 4.90% nitrogen, ranging from a low of 17.4 mg (3.55% sugar) to a high of 23.8 mg (12.80% sugar). The latter (23.8 mg) was the highest mean female adult weight for any sugar/nitrogen combination. At the highest nitrogen level (6.41%), female adult weights no longer increased and were relatively uniform across all sugar levels, ranging from 19.8 mg (6.41% sugar) to 21.1 mg (12.80% sugar).

Pupal Growth Rate

Female pupal growth rate (pupal weight divided by the number of days to reach the pupal stage) is equivalent to biomass accumulated per day. As expected, growth rates for females were significantly lower at 1.38% nitrogen than at all other nitrogen levels (Tables 6,7 and Figures 6,7). Growth rates at this nitrogen level ranged from a low of 1.35 mg/da (38.46% sugar) to a high of 1.94 mg/da (19.23% sugar). On diets containing twice as much nitrogen (2.45%), growth rates increased about 65%, ranging from 2.19 mg/da (38.46% sugar) to 3.28 mg/da (12.80% sugar). At 4.90% nitrogen, growth rates were still larger, ranging from 3.18 mg/da (3.55% sugar) to 4.03 mg/da (12.80% sugar). The latter (4.03 mg/da) was the highest mean female pupal growth rate for any sugar/nitrogen combination. At the highest nitrogen

Table 6. Female pupal growth rate (mg/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	1.68±0.15 n=4 (b,1)*	2.43±0.13 n=34 (b,3)	3.18±0.08 n=162 (a,3)	3.23±0.11 n=91 (a,1)	3.09 (3)
6.41	1.83±0.10 n=8 (c,1)	2.94±0.12 n=57 (b,2)	3.85±0.11 n=128 (a,2)	3.28±0.01 n=104 (b,1)	3.42 (2)
12.80	1.73±0.13 n=13 (c,1)	3.28±0.08 n=91 (b,1)	4.03±0.07 n=202 (a,1)	3.51±0.12 n=102 (b,1)	3.66 (1)
19.23	1.94±0.13 n=11 (c,1)	2.96±0.11 n=64 (b,2)	3.42±0.01 n=99 (a,3)	3.30±0.10 n=109 (a,1)	3.21 (3)
25.64	1.59±0.09 n=4 (c,1)	2.85±0.10 n=53 (b,2)	3.65±0.05 n=422 (a,2)	------	3.55 (2)
38.46	1.35±0.29 n=2 (b,1)	2.19±0.12 n=30 (a,3)	------	------	2.14 (4)
Grand Mean	1.77 (d)	2.90 (c)	3.65 (a)	3.33 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the p < 0.05 level (Ducans multiple range test).

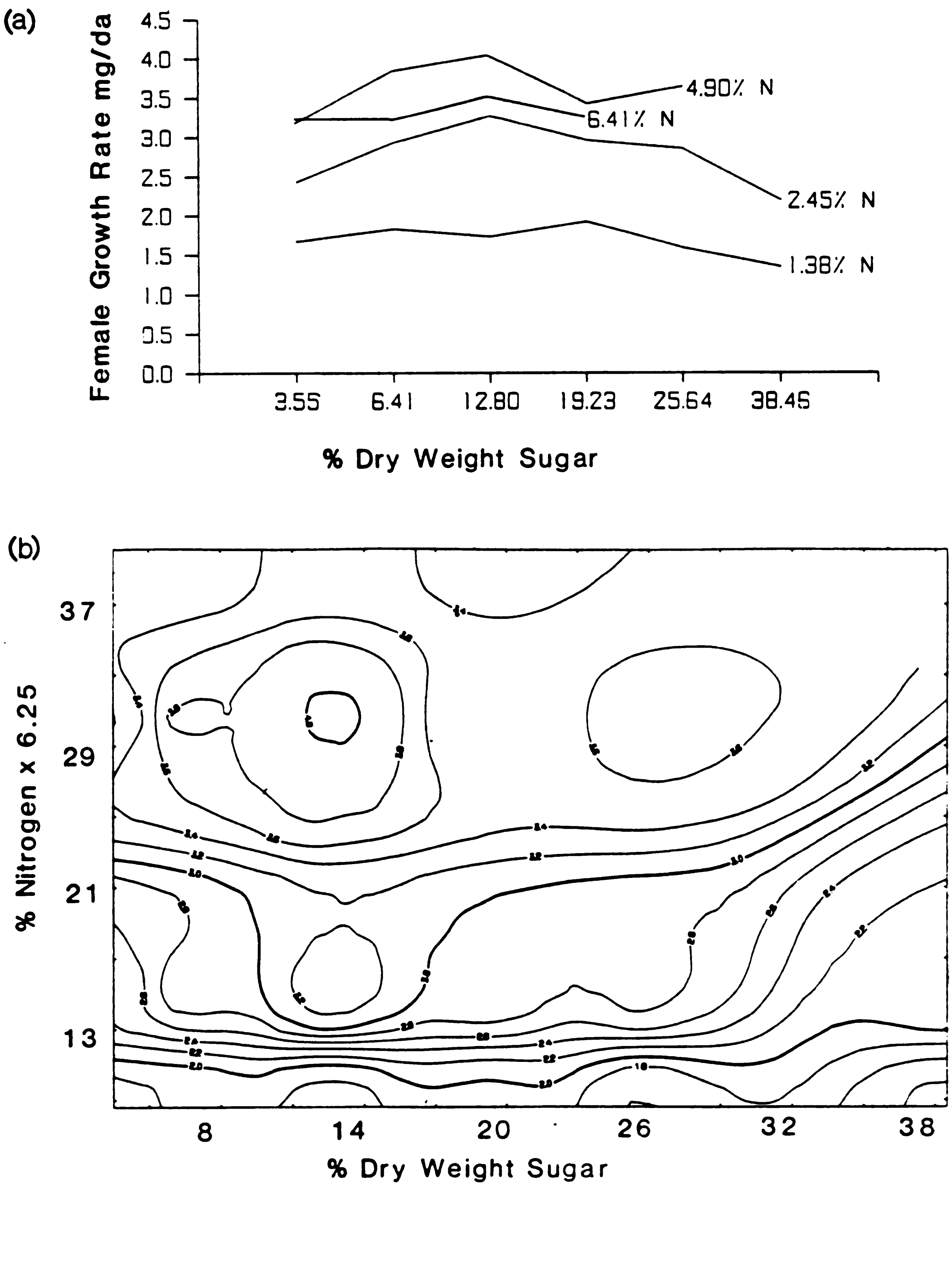


Figure 6. Female pupal growth rate (mg/da) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 7. Male pupal growth rate (mg/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	1.03±0.09 n=6 (c,1,2)*	1.83±0.07 n=56 (b,2)	2.44±0.05 n=183 (a,3)	2.30±0.06 n=104 (a,1)	2.27 (3)
6.41	1.11±0.07 n=18 (c,1,2)	2.21±0.08 n=87 (b,1)	2.80±0.07 n=171 (a,2)	2.38±0.07 n=126 (b,1)	2.46 (2)
12.80	1.26±0.09 n=18 (c,1)	2.35±0.05 n=140 (b,1)	2.98±0.05 n=296 (a,1)	2.45±0.06 n=122 (b,1)	2.66 (1)
19.23	1.24±0.06 n=31 (c,1)	1.87±0.07 n=79 (b,2)	2.29±0.07 n=99 (a,3)	2.38±0.07 n=157 (a,1)	2.15 (4)
25.64	0.99±0.09 n=14 (c,2)	2.01±0.05 n=85 (b,2)	2.44±0.04 n=542 (a,3)	------	2.35 (3)
38.46	0.80±0.16 n=6 (b,2)	1.28±0.07 n=42 (a,3)	------	------	1.22 (5)
Grand Mean	1.14 (d)	2.04 (c)	2.60 (a)	2.38 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p <$ 0.05 level (Ducans multiple range test).

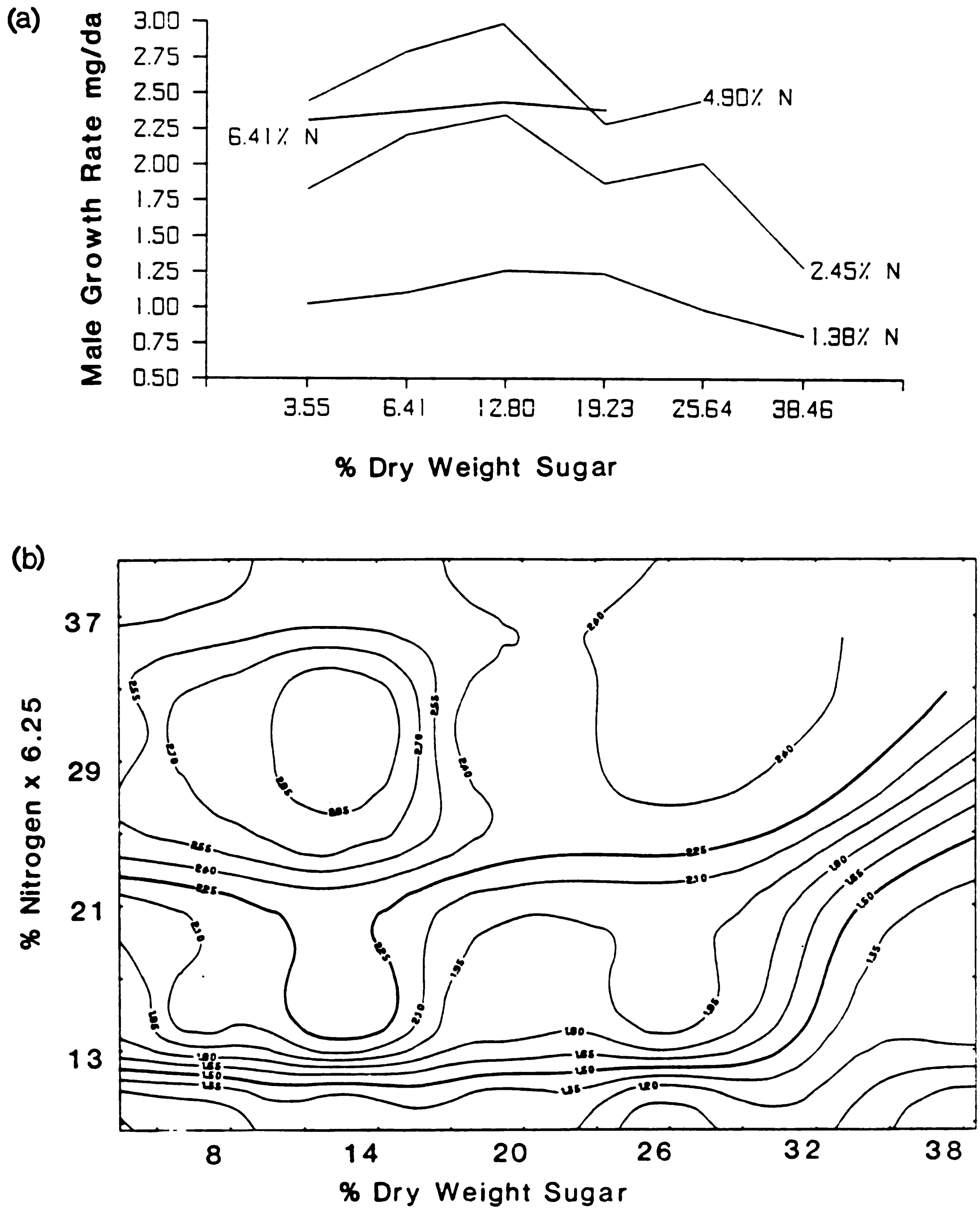


Figure 7. Male pupal growth rate (mg/da) in relationship to dietary levels of sugars and nitrogen (% dw).

level (6.41%), growth rates no longer increased but in fact declined slightly. Values ranged from 3.23 mg/da (3.55% sugar) to 3.51 mg/da (12.80% sugar).

Adult Growth Rates

Female adult growth rate (adult dry weight divided by the number of days to adult eclosion) was lowest at 1.38% nitrogen, ranging from 0.237 mg/da (3.55% sugar) to 0.309 mg/da (19.23% sugar) (Tables 8,9 and Figures 8,9). With twice as much nitrogen (2.45%) in the diet, growth rates increased about 54%, ranging from 0.327 mg/da (3.55% sugar) to 0.468/da (12.80% sugar). On diets containing 4.90% nitrogen, growth rates were still higher, ranging from 0.405 mg/da (3.55% sugar) to 0.617 mg/da (12.80% sugar). The latter (0.617 mg/da) was the highest mean female adult growth rate for any sugar/nitrogen combination. At the highest nitrogen level (6.41%), growth rates declined slightly, ranging from 0.494 mg/da (3.55% sugar) to 0.538 mg/da (12.80% sugar).

Pupal Development Rate

Female pupal development rate (100 divided by the number of days to the pupal stage), is equivalent to percent development per day. As expected, female development rates were significantly lower at 1.38% nitrogen than at all other

Table 8. Female adult growth rate (mg/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	0.237±0.02 n=4 (c,2)*	0.327±0.03 n=22 (c,3)	0.405±0.02 n=62 (b,4)	0.494±0.02 n=78 (a,1)	0.432 (4)
6.41	0.259±0.05 n=5 (c,2)	0.409±0.02 n=79 (b,2)	0.491±0.01 n=111 (a,3)	0.512±0.02 n=95 (a,1)	0.472 (3)
12.80	0.301±0.03 n=9 (d,2)	0.468±0.01 n=96 (c,1)	0.617±0.01 n=131 (a,1)	0.538±0.02 n=85 (b,1)	0.543 (1)
19.23	0.309±0.03 n=10 (c,2)	0.466±0.02 n=54 (b,1)	0.550±0.02 n=89 (a,2)	0.526±0.02 n=89 (a,1)	0.512 (2)
25.64	0.236±0.03 n=4 (c,2)	0.443±0.02 n=67 (b,1,2)	0.588±0.01 n=358 (a,1)	------	0.562 (1)
38.46	0.268±0.00 n=1 (b,1)	0.346±0.02 n=26 (a,3)	------	------	0.343 (5)
Grand Mean	0.280 (d)	0.431 (c)	0.559 (a)	0.518 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the p < 0.05 level (Ducans multiple range test).

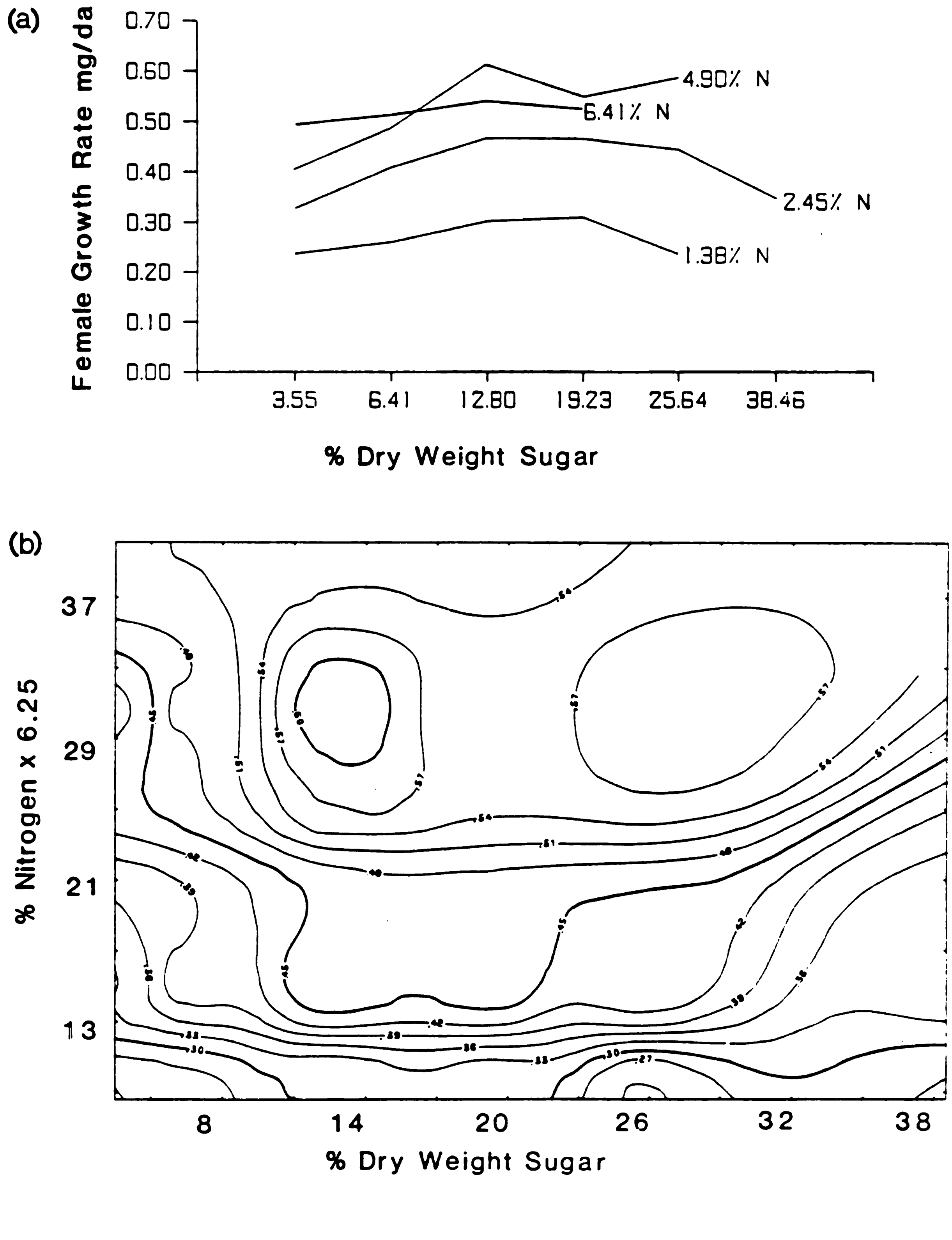


Figure 8. Female adult growth rate (mg/da) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 9. Male adult growth rate (mg/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	0.103±0.01 n=6 (d,3)*	0.189±0.01 n=34 (c,3,4)	0.225±0.01 n=43 (b,4)	0.266±0.01 n=90 (a,2)	0.235 (4)
6.41	0.156±0.01 n=13 (c,2)	0.204±0.01 n=87 (b,3)	0.269±0.01 n=160 (a,3)	0.272±0.01 n=104 (a,1,2)	0.250 (3,4)
12.80	0.171±0.02 n=9 (d,2)	0.248±0.01 n=117 (c,1)	0.319±0.01 n=125 (a,1)	0.292±0.01 n=98 (b,1)	0.284 (1)
19.23	0.157±0.01 n=13 (c,2)	0.227±0.01 n=69 (b,1,2)	0.273±0.01 n=89 (a,2,3)	0.276±0.01 n=121 (a,1,2)	0.258 (3)
25.64	0.108±0.02 n=6 (c,3)	0.241±0.01 n=68 (b,1,2)	0.286±0.01 n=472 (a,2)	------	0.279 (2)
38.46	0.163±0.00 n=1 (b,1)	0.172±0.01 n=28 (a,4)	------	------	0.172 (5)
Grand Mean	0.147 (c)	0.223 (b)	0.284 (a)	0.276 (a)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

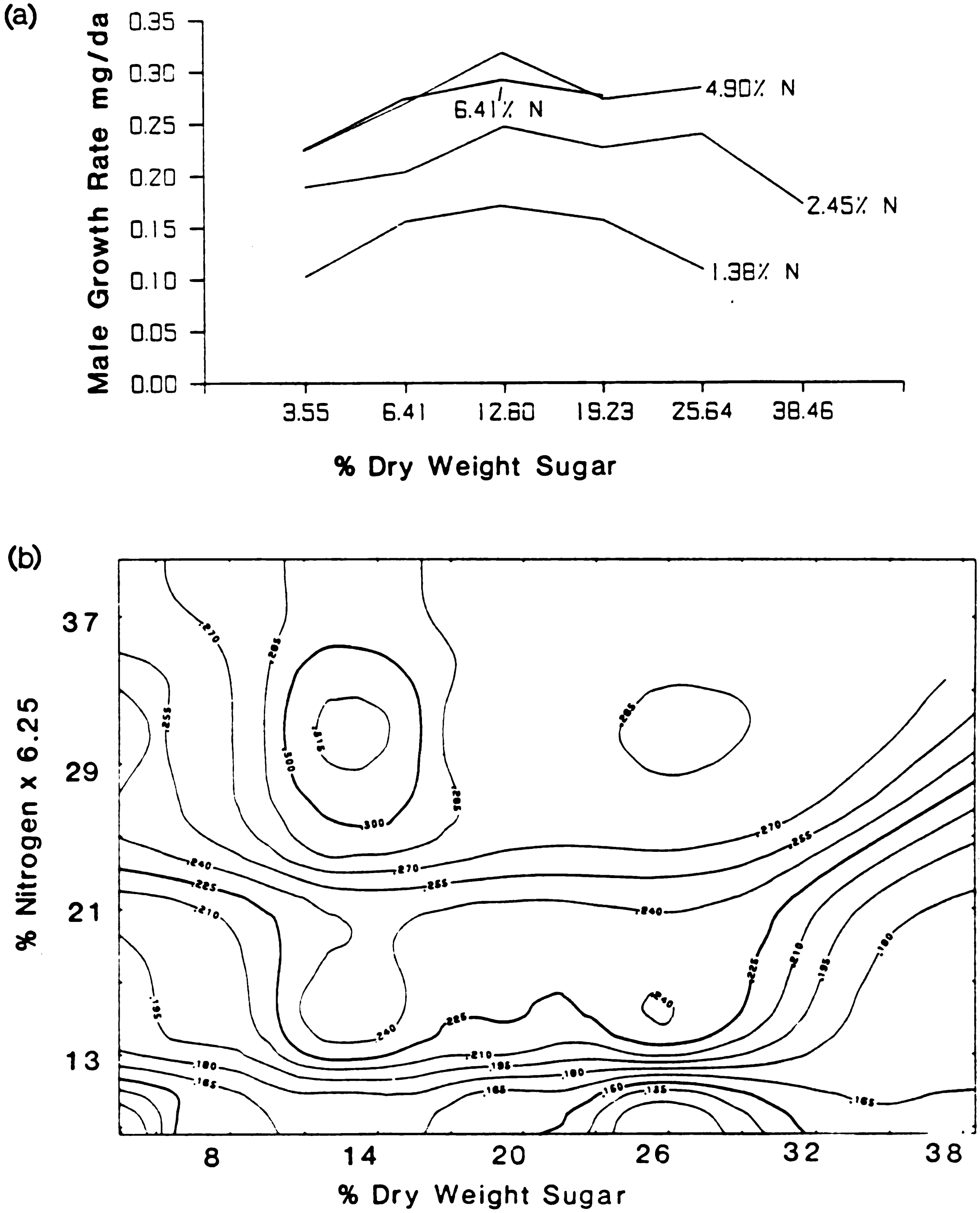


Figure 9. Male adult growth rate (mg/da) in relationship to dietary levels of sugars and nitrogen (% dw).

nitrogen levels (Tables 10,11 and Figures 10,11). Growth rates at this nitrogen level ranged from a low of 2.02%/da (38.46% sugar) to a high of 2.35%/da (6.41% sugar). On diets containing twice as much nitrogen (2.45%), development rates were about 22% faster ranging from 2.45%/da (38.46% sugar) to 2.91%/da (12.80% sugar). On diets containing 4.9% nitrogen, development rates were still faster, rangingfrom 3.18%/da (3.55 and 38.46% sugar) to 3.47%/da (12.80 % sugar). The latter (3.47%/da) was the highest mean female pupal development rate for any sugar/nitrogen combination. At the highest nitrogen level (6.41%), development rates no longer increased significantly, ranging from 3.12%/da (3.55% sugar) to 3.26%/da (6.41% sugar)

Adult Development Rate

Female adult development, as was true for female pupae, was much slower on diets containing 1.38% nitrogen, ranging from 1.67%/da (38.46% sugar) to 1.94%/da (12.80% sugar), (Tables 12,13 and Figures 12,13). On diets containing twice as much nitrogen (2.45%), development rates increased about 14%, ranging from 2.01%/da (38.46% sugar) to 2.25%/da (12.80% sugar). Development rates on diets containing 4.90% nitrogen were even faster, ranging from 2.30%/da (3.55% sugar) to 2.59%/da (12.80% sugar). The latter (2.59%/da) was the highest mean female adult develpment rate for any

Table 10. Female pupal development rate (%/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	2.25±0.18 n=4 (c,1)*	2.73±0.06 n=34 (b,2,3)	3.18±0.03 n=162 (a,3)	3.12±0.04 n=91 (a,2)	3.10 (2)
6.41	2.35±0.08 n=8 (c,1)	2.81±0.04 n=110 (b,2)	3.30±0.04 n=167 (a,2)	3.26±0.04 n=104 (a,1)	3.13 (2)
12.80	2.27±0.05 n=13 (d,1)	2.91±0.03 n=143 (c,1)	3.47±0.02 n=285 (a,1)	3.23±0.04 n=102 (b,1)	3.25 (1)
19.23	2.30±0.07 n=11 (c,1)	2.71±0.05 n=64 (b,2,3)	3.20±0.04 n=99 (a,2,3)	3.25±0.04 n=109 (a,1)	3.07 (1)
25.64	2.19±0.07 n=4 (c,1)	2.62±0.03 n=85 (b,3)	3.18±0.02 n=480 (a,3)	------	3.09 (2)
38.46	2.02±0.02 n=2 (b,1)	2.45±0.05 n=30 (a,4)	------	------	2.42 (3)
Grand Mean	2.27 (d)	2.76 (c)	3.27 (a)	3.22 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p <$ 0.05 level (Ducans multiple range test).

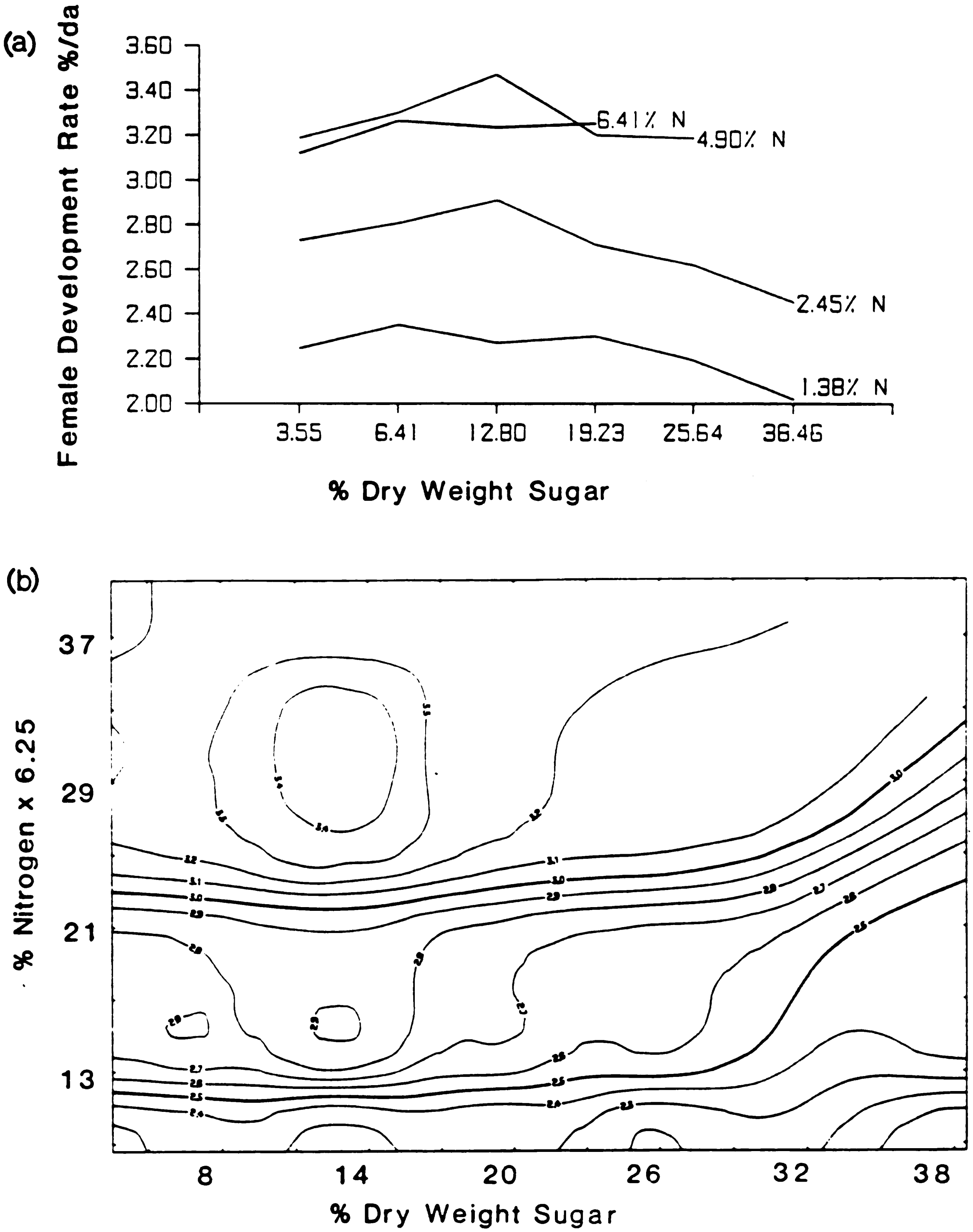


Figure 10. Female pupal development rate (%/da) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 11. Male pupal development rate (%/da) $\pm$ standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	2.40±0.13 n=6 (d,1,2)*	2.88±0.05 n=56 (c,3)	3.52±0.03 n=183 (a,3)	3.37±0.04 n=104 (b,2)	3.35 (2)
6.41	2.37±0.06 n=18 (d,1,2)	3.08±0.04 n=147 (c,2)	3.64±0.04 n=238 (a,2)	3.52±0.04 n=126 (b,1)	3.41 (2)
12.80	2.42±0.08 n=18 (d,1,2)	3.17±0.03 n=188 (c,1)	3.78±0.03 n=364 (a,1)	3.52±0.04 n=122 (b,1)	3.53 (1)
19.23	2.47±0.05 n=31 (c,1)	2.82±0.05 n=79 (b,3)	3.41±0.05 n=99 (a,3,4)	3.42±0.03 n=157 (a,1,2)	3.21 (3)
25.64	2.24±0.05 n=14 (c,2)	2.91±0.03 n=107 (b,3)	3.35±0.02 n=622 (a,4)	------	3.27 (3)
38.46	2.15±0.08 n=6 (b,2)	2.60±0.06 n=42 (a,3)	------	------	2.54 (4)
Grand Mean	2.38 (d)	2.99 (c)	3.52 (a)	3.46 (b)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

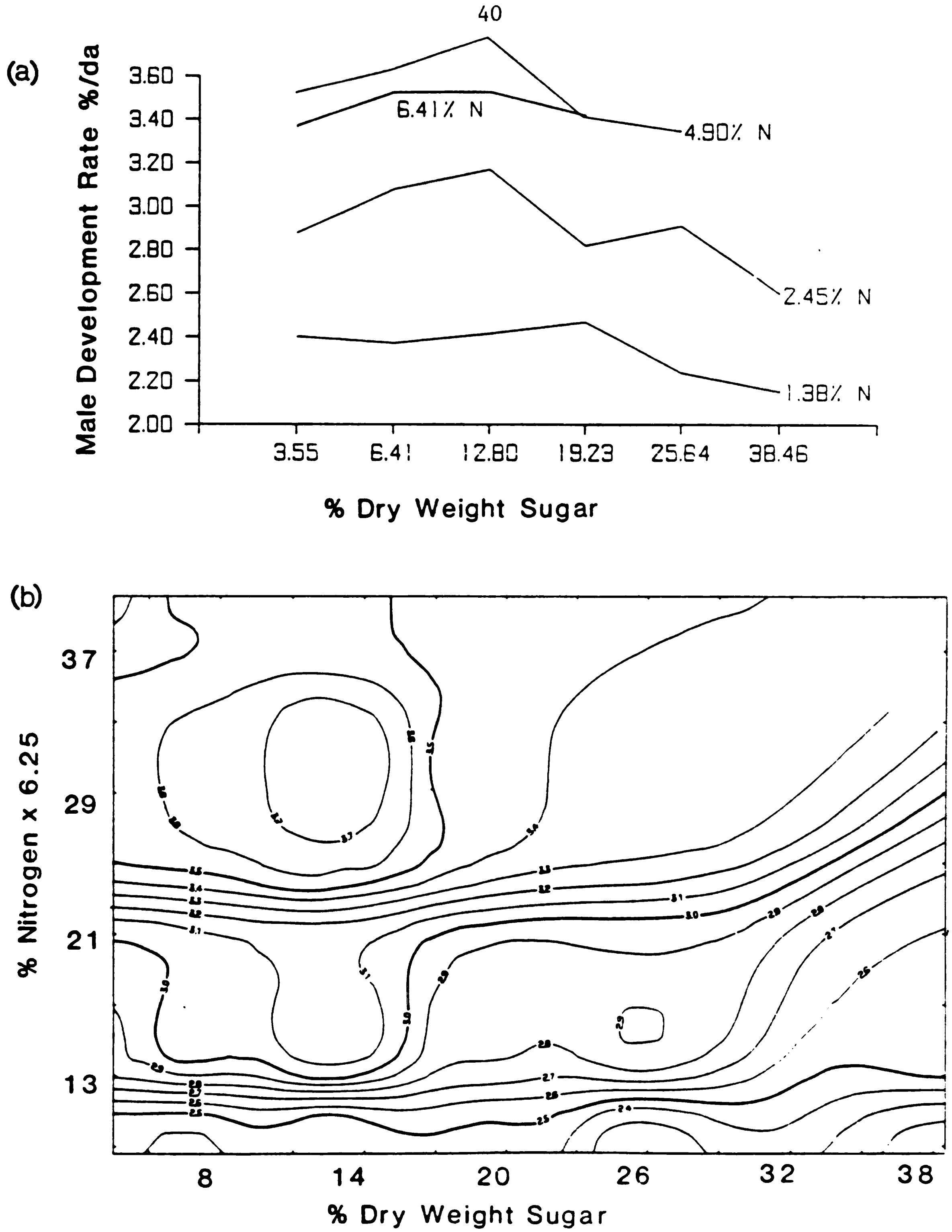


Figure 11. Male pupal development rate (%/da) in relationshp to dietary levels of sugars and nitrogen (% dw).

Table 12. Female adult development rate (%/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	1.89±0.13 n=4 (c,2)*	2.19±0.05 n=22 (b,1,2)	2.30±0.03 n=62 (b,3)	2.44±0.03 n=79 (a,2)	2.34 (2)
6.41	2.02±0.07 n=5 (c,2)	2.19±0.02 n=79 (c,1)	2.44±0.02 n=111 (b,2)	2.57±0.03 n=95 (a,1)	2.40 (1)
12.80	1.94±0.06 n=9 (d,2)	2.25±0.02 n=96 (c,1)	2.59±0.02 n=131 (a,1)	2.52±0.03 n=85 (b,1)	2.45 (1)
19.23	1.91±0.06 n=10 (c,2)	2.19±0.03 n=54 (b,1,2)	2.56±0.03 n=89 (a,1)	2.55±0.03 n=89 (a,1)	2.45 (1)
25.64	1.84±0.06 n=4 (c,2)	2.11±0.02 n=67 (b,2)	2.48±0.01 n=359 (a,2)	------	2.42 (1)
38.46	1.67±0.00 n=1 (b,1)	2.01±0.04 n=26 (a,3)	------	------	1.99 (3)
Grand Mean	1.92 (d)	2.18 (c)	2.49 (b)	2.52 (a)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

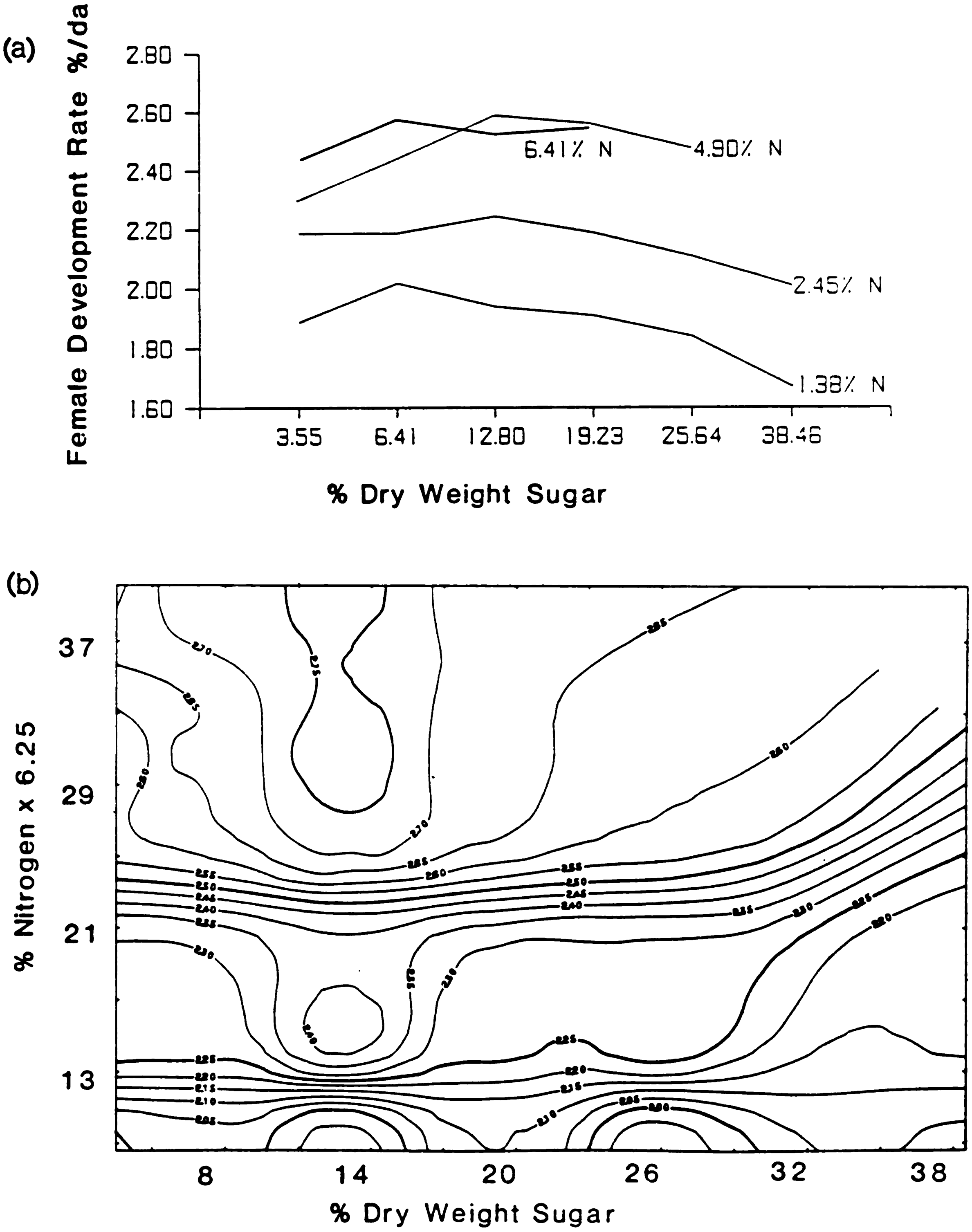


Figure 12. Female adult development rate (%/da) in relationship to dietary levels of sugars and nitrogen (% dw).

Table 13. Male adult development rate (%/da) ± standard error and number of insects surviving per treatment.

Sugar % dw	Nitrogen % Dry Weight 1.38	2.45	4.90	6.41	Grand Mean
3.55	1.99 0.10 n=6 (c,2)*	2.29 0.04 n=34 (b,2,3)	2.56 0.04 n=43 (a,2)	2.64 0.03 n=90 (a,2)	2.53 (2)
6.41	2.03±0.04 n=13 (d,2)	2.28±0.03 n=87 (c,2)	2.66±0.02 n=160 (b,2)	2.74±0.03 n=104 (a,1)	2.57 (2)
12.80	1.93±0.08 n=9 (c,2)	2.42±0.03 n=117 (b,1)	2.77±0.02 n=125 (a,1)	2.76±0.03 n=98 (a,1)	2.63 (1)
19.23	2.10±0.05 n=13 (c,2)	2.27±0.03 n=69 (b,2,3)	2.67±0.04 n=89 (a,2)	2.67±0.02 n=121 (a,2)	2.55 (2)
25.64	1.92±0.05 n=6 (c,2)	2.29±0.03 n=68 (b,2)	2.60±0.02 n=475 (a,2)	------	2.55 (2)
38.46	2.04±0.00 n=1 (b,1)	2.16±0.05 n=28 (a,3)	------	------	2.16 (3)
Grand Mean	2.01 (d)	2.31 (c)	2.64 (b)	2.70 (a)	

* Means followed by the same letter (within rows) or number (within columns) are not significantly different at the $p < 0.05$ level (Ducans multiple range test).

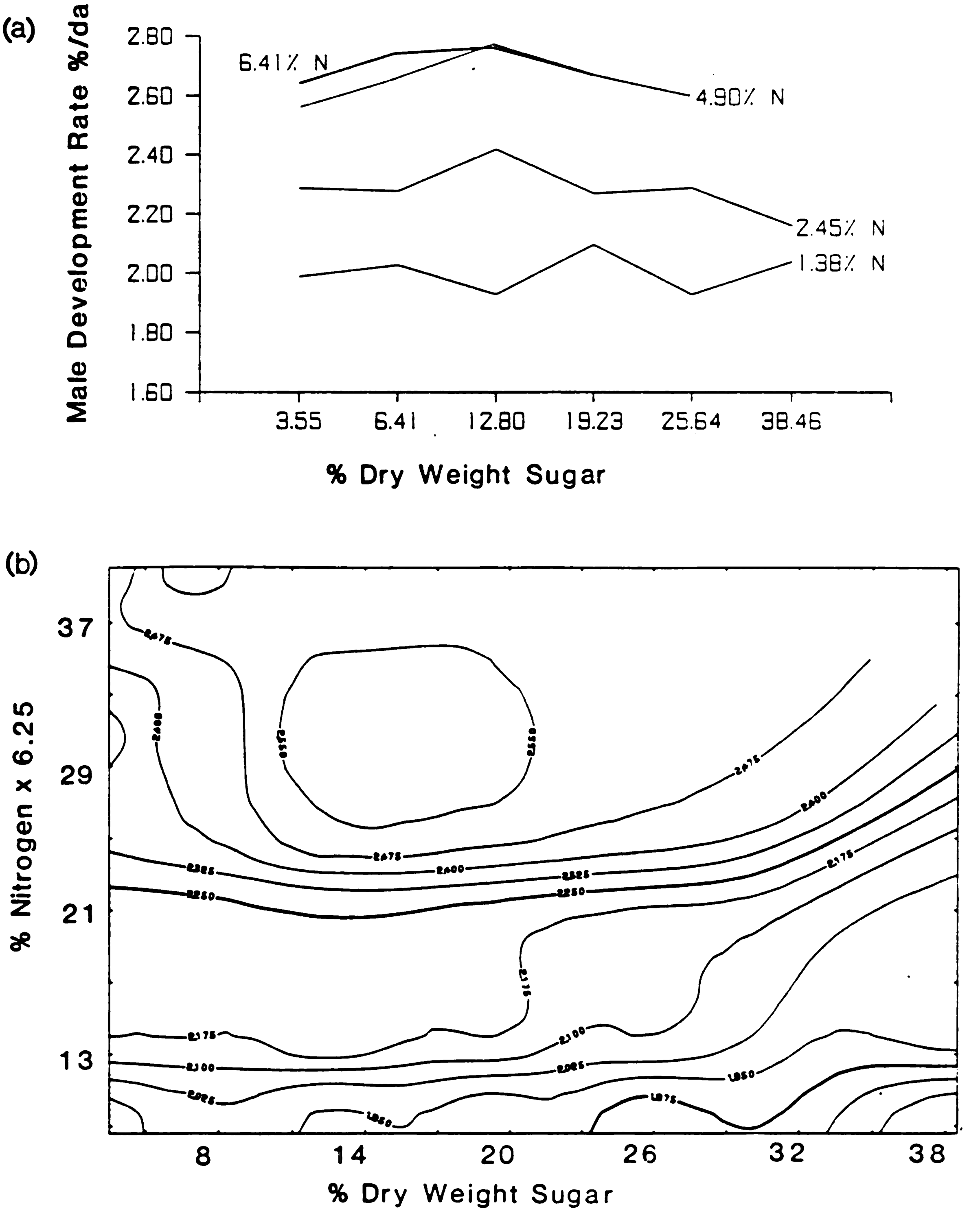


Figure 13. Male adult development rate (%/da) in relationship to dietary levels of sugars and nitrogen (% dw).

sugar/nitrogen combination. At the highest nitrogen level (6.41%), development rates decreased only slightly ranging from 2.44%/da (3.55% sugar) to 2.57%/da (6.41% sugar).

Optimal Ratios of Sugar to Nitrogen at Different Nitrogen Levels

As before, performance of male and female budworm followed similar patterns among all treatments. Hence, to avoid unneccessary discussion only female responses will be presented for the following parameters; pupal fresh weight gain, pupal growth rate (mg/da) and pupal development rate (%/da). Data for all sexes and all parameters are, however, demonstrated in the tables and figures. Optimal ranges were determined using Duncans multiple range test. Ranges on diets containing 1.38% nitrogen were very broad. This was due in part to the small sample size which resulted because of poor survival on these diets. For example, data from diets containing 1.38% nitrogen and 38.46% sugar were not included because sample size was so small (n=2 survivors).

Pupal Fresh Weight

On diets containing 1.38% nitrogen, optimal sugar/nitrogen ratios ranged from 2.59/1 to 18.67/1 (midpoint 10.63/1) (Figure 14). On diets containing twice as much nitrogen (2.45%), the range for optimal sugar/nitrogen ratios was from 5.24/1 to 10.49/1 (midpoint 7.87/1). On

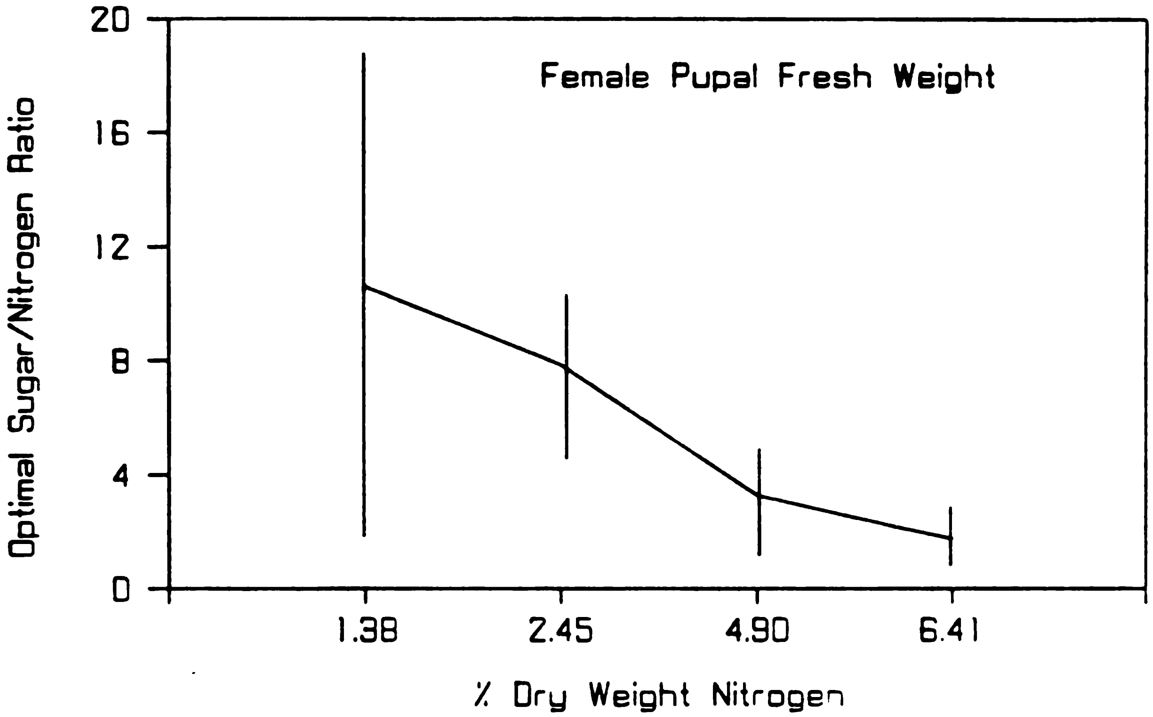


Figure 14. Optimal ratios of sugar to nitrogen at different nitrogen levels in relationship to female pupal weight (mg).

diets containing 4.90% nitrogen, the optimal ratio ranged from 1.31/1 to 5.23/1 (midpoint 3.27/1). At the highest level of nitrogen (6.41%), the range of optimal ratios was smallest, extending from 0.55/1 to 3.0/1 (midpoint 1.78/1).

Pupal Growth Rate (mg/da)

Female pupal growth rates followed a pattern similar to that for female pupal fresh weight (Figure 15). On diets containing 1.38% nitrogen, the optimal sugar/nitrogen ratio extended from 2.59/1 to 18.67/1 (midpoint 10.63). On diets containing 2.45% nitrogen, the optimal sugar/nitrogen ratio was a single point (5.24/1), just as it was for diets containing 4.90% nitrogen (2.61/1). At the highest level of nitrogen (6.41%), optimal ratios extended from 0.55/1 to 3.0/1 (midpoint 1.78/1).

Pupal Development Rate (%/da)

Female pupal development rates followed patterns that were very similar to both pupal weight and pupal growth rate (Figure 16). On diets containing 1.38% nitrogen, the optimal sugar to nitrogen ratio extended from 2.59/1 to 18.67/1 (midpoint 10.63/1). On diets with the next highest nitrogen content (2.45%), the optimal sugar/nitrogen ratio was again a single point (5.24/1), just as it was for diets containing 4.90% nitrogen (2.61/1). At the highest level of nitrogen

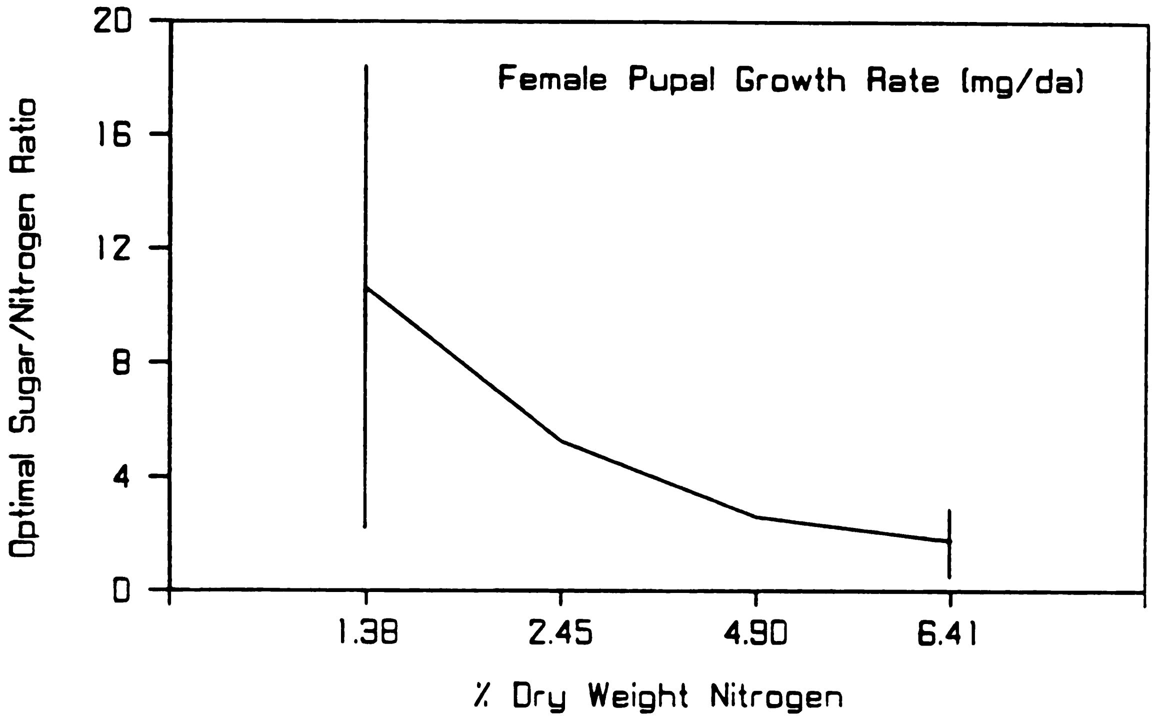


Figure 15. Optimal ratios of sugar to nitrogen at different nitrogen levels in relationship to female pupal growth rate (mg/da).

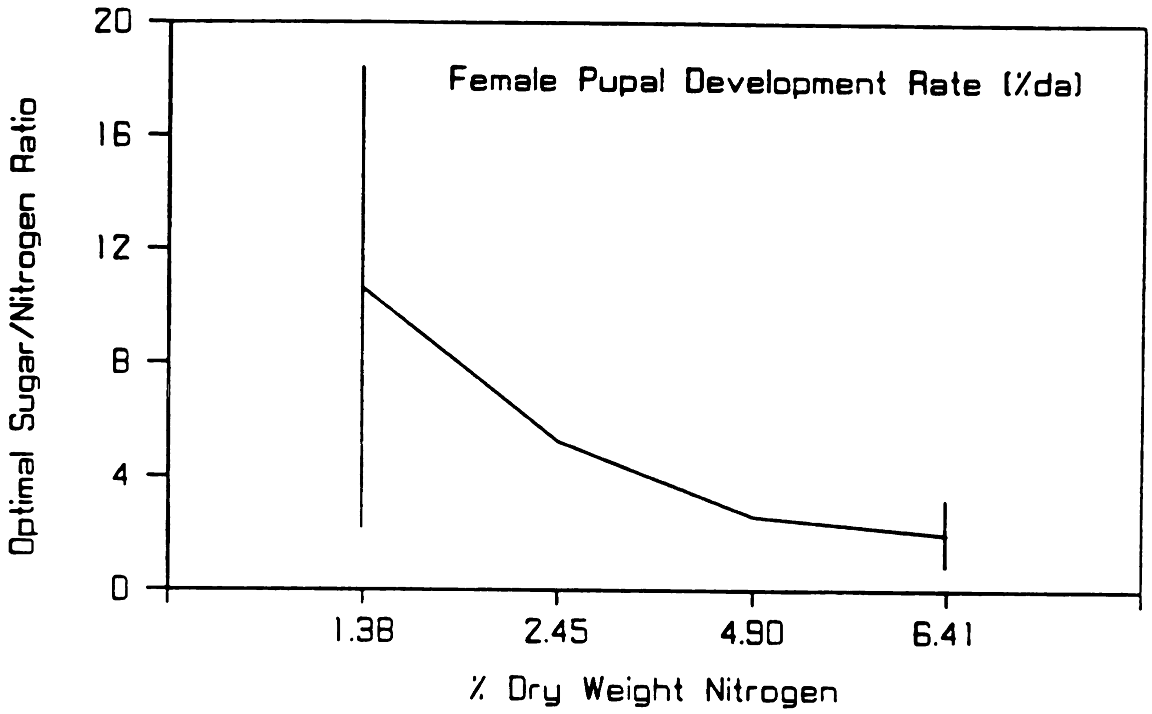


Figure 16. Optimal ratios of sugar to nitrogen at different nitrogen levels in relationship to female pupal development rate (%/da).

(6.41%), optimal ratios extended from 1.0/1 to 3.0/1 (midpoint 2.0/1).

Regression Relationships Between Insect Performance and Dietary Sugar and Nitrogen Concentrations

In order to find a likely mathematical relationship between budworm performance and the various levels of nitrogen and sugar in it's diet, I regressed the seven measures of performance (survival, pupal weight, adult weight, pupal growth rate, adult growth rate, pupal development rate, and adult development rate) on the linear, log and the squared measures of these two nutrients (Table 14). I used the log and squared values because it was evident from the figures (1-13) that performance was probably not linear with respect to these nutrients but was some type of dome-shaped function.

The results of the regression analyses (Table 14) showed a rather clear and consistent pattern. Sugar and nitrogen entered into regression equations only as their log or their squared concentrations. The most general patterns were for insect performance variables to be a function of all four variables; log N, log S, $-N^2$ and $-S^2$ (4 cases) or a binary subset of them: log N, log S (4 cases) and log N, $-N^2$ (2 cases). In just two cases, only one variable (log N) was significant, whereas in one case, three variables (log N, log S, $-S^2$) were. For any given performance variable (e.g.

Table 14. Regression relationshps between insect performance variables and dietary nitrogen and sugar ($p \leq .05$).

Performance Variable[1]	Coefficients for diet nutrient Variables				
	Log N	N^2	Log S	S^2	R^2
Survival Rate	60.88	-1.12			.90
Pupal Weight(F)	49.05	-1.25			.82
Pupal Weight(M)	35.91	-0.94	6.03	-0.18	.95
Adult Weight(F)	9.04	-0.20	4.49	-0.24	.85
Adult Weight(M)	2.02				.55
P.Growth Rate(F)	2.33	-0.51	0.38	-0.89	.96
P.Growth Rate(M)	1.82	-0.41	0.23	-0.73	.94
A.Growth Rate(F)	0.18		0.34		.82
A.Growth Rate(M)	0.92				.80
P.Dev.Rate(F)	1.25		0.23		.93
P.Dev.Rate(M)	1.43		0.25		.91
A.Dev.Rate(F)	0.32		0.14	-0.14	.93
A.Dev.Rate(M)	0.48				.94

[1] (F)= Female, (M)= Male, P. = Pupal, A. = Adult

pupal weight), the equations for males and females were usually not exactly alike. This implies that both sexes are not equally responsive to these two nutrients. However, it is clear that insects respond in a nonlinear manner to changing levels of these two classes of nutrients. If the general performance (P) of the budworm is a function of all four variables such that $P = a_1 \log N - b_1 N^2 + a_2 \log S - b_2 S^2$ then the optimal performance for one nutrient, holding the other constant can be described by taking the partial derivative of this equation with respect to the variable nutrient (V) and then setting it equal to zero and solving for V. The result is the following:

$$V_{opt} = \sqrt{a_i / 2b_i}$$

The equation says that the optimal value for the nutrient (V) will be equal to the square root of it's "a_i" coefficient divided by two times it's "b_i" coefficient.

Concentration of Sugars Remaining In Budworm Frass

Budworm frass was analyzed for soluble sugar content (HPLC analysis). Soluble sugars found in frass were in the form of fructose and glucose. At the very highest sugar level (38.46%) budworm frass contained about 8% dw sugar at both nitrogen levels (Figure 17). At sugar levels

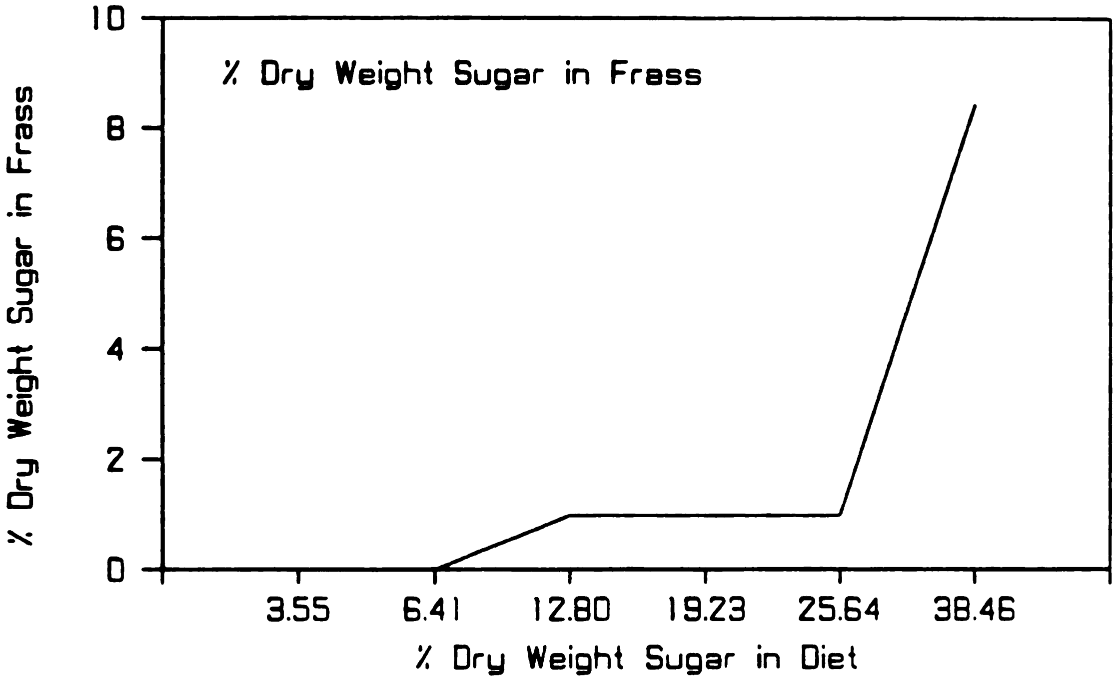


Figure 17. Percent dry weight sugar left in frass in relationship to percent dry weight sugar in artificial diet.

less than or equal to 25.64%, budworm frass contained only 1% sugar or less at all nitrogen levels. Frass from diets containing 6.41% sugar or less at all nitrogen levels contained virtually no soluble sugars at all.

Addition of Fatty Acids to Low Level Nitrogen Diets

Fatty acid were added to diets containing 2.45% nitrogen in the form of either wheat germ oil or indivdually (linoleic and linolenic acids). These oils were added via an acetone solvent to the casein portion of the diet media. Oils were added in ammounts which compensated for the loss of fatty acids when nitrogen levels were reduced from 4.91% to 2.45% by reducing the wheat germ content of the diet. Female pupal weights were significantly higher for all sugar levels on control diets (2.45% nitrogen with no added oils) than on diets containing 2.45% nitrogen with added wheat germ oil or added linoleic and linolenic acids (Table 15).

Table 15. Female pupal weight (mg) on diets containing 2.45% nitrogen, 2.45% nitrogen with linoleic and linolenic acids and 2.45% nitrogen with wheat germ oil. Levels where blanks (----) occur indicate zero percent survival.

Sugar % dry weight	Nitrogen % Dry Weight[1] 2.45%	2.45 w/fa	2.45% w/oil
3.55	87.8±4.0 n=34	------	------
6.41	98.6±3.1 a n=57	89.6±3.7 b n=16	76.5±4.2 c n=8
12.80	107.0±2.1 a n=91	88.6±2.9 b n=37	81.7±5.1 b n=15
19.23	108.2±3.2 a n=64	94.9±4.6 b n=21	95.6±3.8 b n=23
25.64	105.2±2.9 a n=53	90.5±3.9 b n=19	92.1±5.2 b n=20
38.46	88.7±4.1 a n=30	57.7±2.5 b n=29	69.5±2.8 b n=16
Grand Mean	101.8	84.2	83.3

[1] Means followed by the same letters across rows are not significantly different at the $p \leq .05$ level (Duncans multiple range test).

Field Studies

Balsam Fir and White Spruce Foliar Sugar and Nitrogen Concentrations in Relation to (^{o}D) Accumulations

Three major sugars were found in current year foliage of balsam fir and white spruce throughout the entire time of budworm feeding: fructose, glucose and sucrose. Hereafter, sugar concentrations refer to the sum total of these three sugars.

Balsam fir foliar sugar concentration was about 5.2% dwt just after budworm emergence and during needle mining (220 ^{o}D; see ^{o}D estimation technique in Mattsonet al. 1983) (Figure 18). Foliar sugar concentration declined slightly and then gradually increased to a maximum of 6.2% dwt (630 ^{o}D) when budworm were sixth instars. Ninety percent of budworm feeding occurs while they are fifth and sixth instars. Minimum foliar sugar concentration was 3.0% dwt (300 ^{o}D).

For white spruce, foliar sugar concentrations followed a pattern like that of fir but were much more variable, ranging from 6.1% dwt (220 ^{o}D) during budworm needle mining, increasing to a high of about 20.2% and then declining to 10.1% dwt (630 ^{o}D) when budworm were in the sixth instar (Figure 18). Minimum concentration was 5.0% dwt (300 ^{o}D) and maximum concentration was 20.8% dwt (480

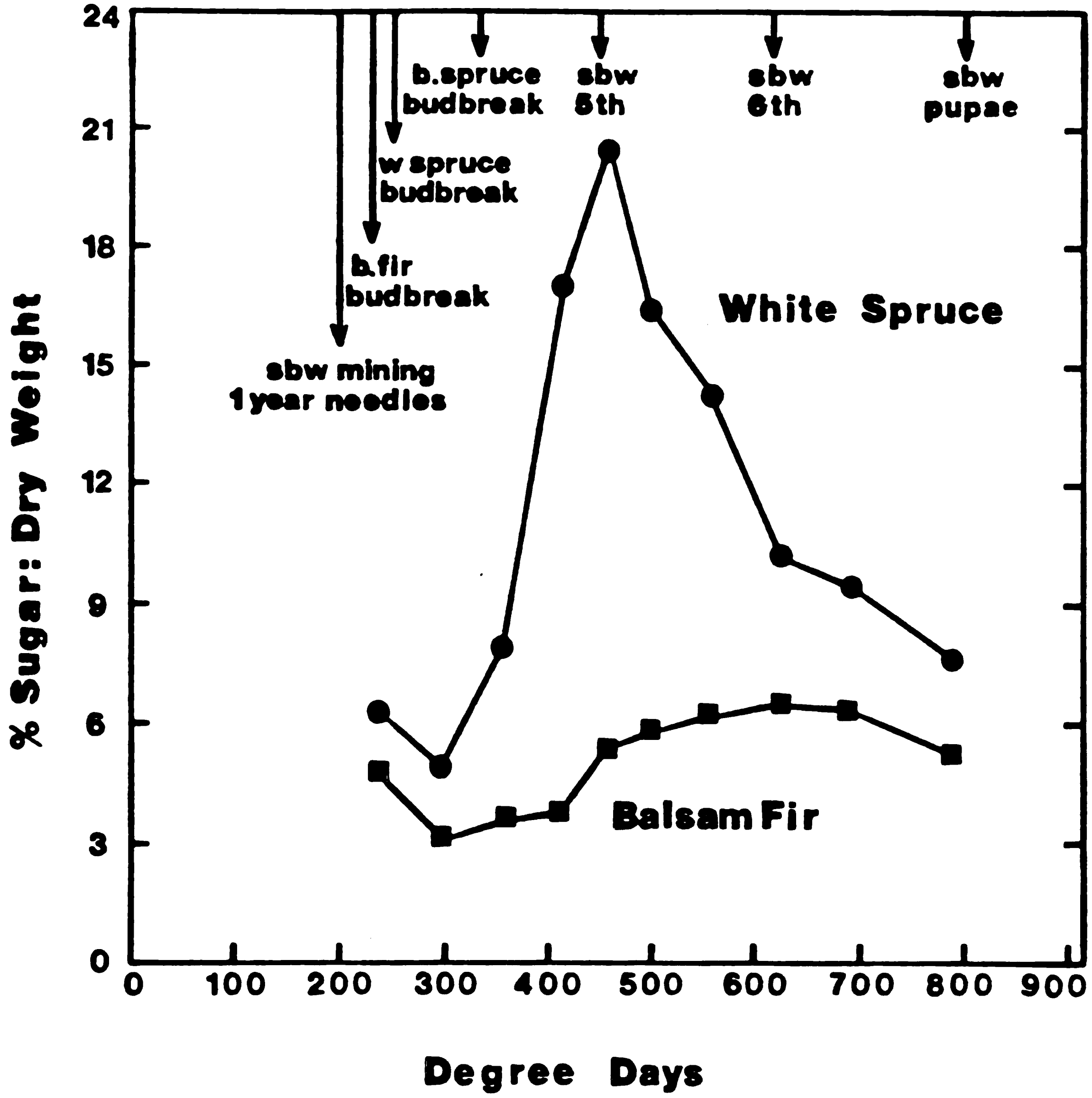


Figure 18. Balsam fir and white spruce foliar sugar concentration in relation to degree day accumulaton.

^{o}D).

In contrast, balsam fir and white spruce foliar nitrogen concentrations showed a steady exponential decay throughout the growing season (Figure 19). For balsam fir, there was a maximum concentration of 5.5% dw (220 ^{o}D) just after budworm emergence and 1.7% dw (630 ^{o}D) when budworm were sixth instars. For white spruce, there was a maximum concentration of 6.6% dw (220 ^{o}D) at budworm emergence and 1.1% dw (630 ^{o}D) when budworms were sixth instars.

Balsam fir foliar sugar/nitrogen ratios ranged from 0.95/1 (220 ^{o}D) to 4.13/1 (700 ^{o}D). White spruce foliar sugar/nitrogen ratios ranged from 0.94/1 (220 ^{o}D) to 13.0/1 (480 ^{o}D).

Concentrations of Nitrogen and Sugars During Fifth and Sixth Larval Stages

Northern Minnesota

Mean foliar nitrogen concentrations of balsam fir during thebudworm's fifth and sixth larval stages between 1981 and 1984 ranged from 1.30% dw (1981) to 1.86% dw (1984), (Tables 16,17). Mean total foliar sugar values ranged from 2.88% dw (1981) to 8.12% dw (1983). Mean sugar/nitrogen ratios extended from a low of 1.92/1 in 1981 to a high of 5.76/1 in 1983. Black spruce trees in 1981 and 1982 had mean foliar nitrogen values of 0.75% dw (1981) and

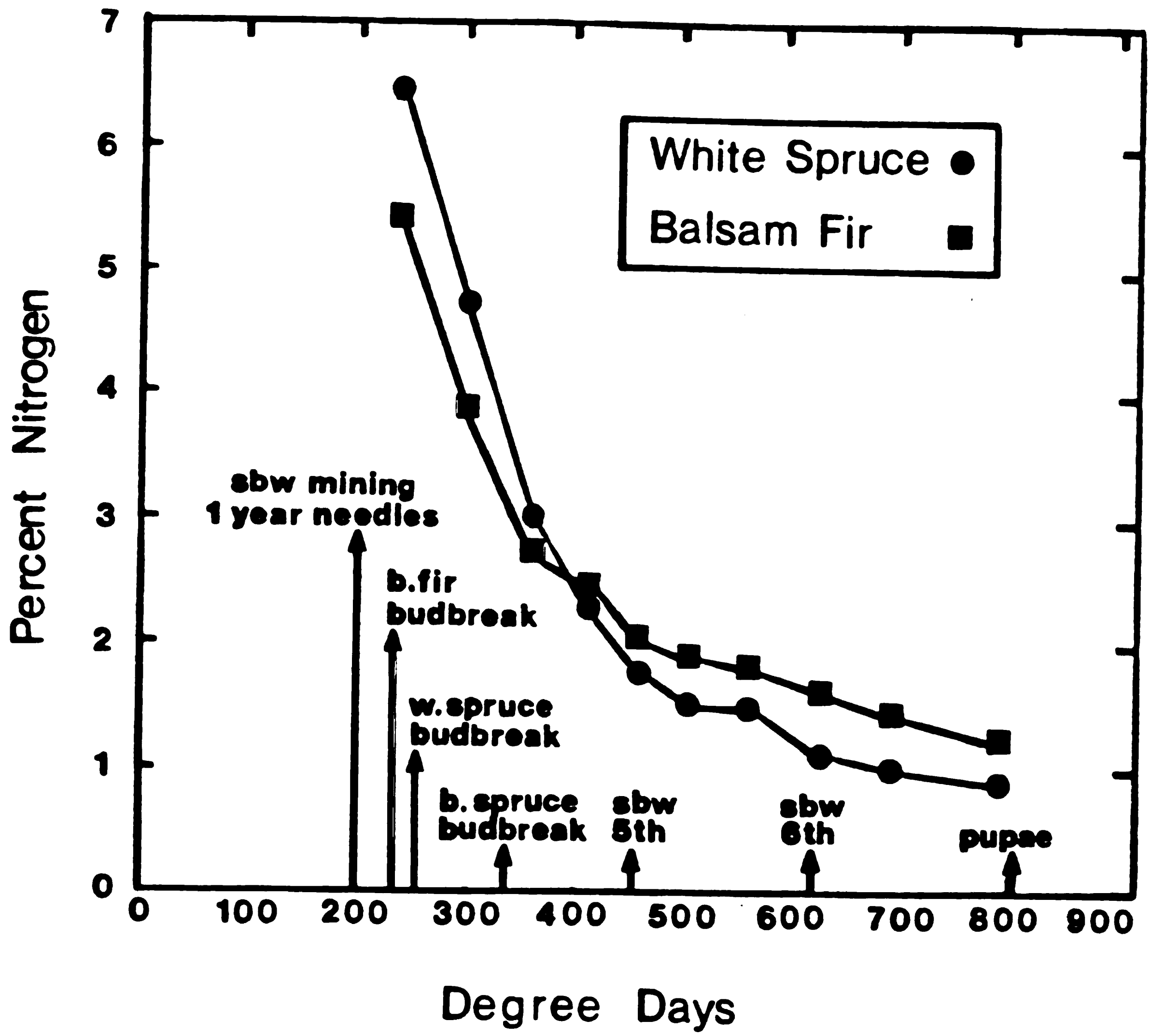


Figure 19. Balsam fir and white spruce foliar nitrogen concentration in relation to degree day accumulation.

Table 16. Grand mean values $\pm$ standard error for nitrogen, sugar and sugar/nitrogen ratios for field studies performed from 1981-1982. n= number of trees per study.

Study Area/Yr/Tree Sp.[1]	N Mean	S Mean	S/N Mean
I. Falls 1981 B.F.	1.55$\pm$0.04 n=31	2.88$\pm$0.16 n=31	1.92$\pm$0.14
I. Falls 1982 B.F.	1.30$\pm$0.03 n=30	4.17$\pm$0.51 n=30	3.24$\pm$0.40
I. Falls 1981 W.S.	1.24$\pm$0.04 n=18	3.32$\pm$0.23 n=18	2.70$\pm$0.18
I. Falls 1982 W.S.	1.20$\pm$0.03 n=20	3.67$\pm$0.44 n=20	3.03$\pm$0.33
Cromwell 1981 Bk.S.	0.75$\pm$0.04 n=16	3.50$\pm$0.33 n=16	4.84$\pm$0.53
Cromwell 1982 Bk.S.	0.85$\pm$0.02 n=15	3.92$\pm$0.40 n=15	4.64$\pm$0.49

[1] I.= International, B.F.= balsam fir, W.S.= white spruce, Bk.S. = black spruce

Table 17. Grand mean values ± standard error for nitrogen, sugarand sugar/nitrogen ratios for field studies performed from 1983-1984. n= number of trees per study.

Study Area/Yr/Tree Sp.[1]	N Mean	S Mean	S/N Mean
Kellogg 1983 B.F.	1.60±0.02 n=20	5.42±0.86 n=20	3.34±0.48
Kellogg 1984 B.F.	1.90±0.05 n=34	4.20±0.52 n=34	2.32±0.30
I. Falls 1983 B.F.	1.41±0.04 n=10	8.12±0.46 n=10	5.76±0.24
I. Falls 1984 B.F.	1.86±0.04 n=14	7.64±0.29 n=14	4.12±0.14
Antigo 1984 B.F.	2.84±0.11 n=28	6.86±0.60 n=28	2.60±0.26
Kellogg 1983 W.S.	1.38±0.03 n=33	9.63±0.80 n=33	6.95±0.52
Kellogg 1984 W.S.	1.80±0.05 n=32	3.25±0.42 n=32	1.85±0.27
Wellston 1984 W.S.	2.24±0.05 n=34	7.13±0.42 n=34	3.23±0.20

[1] B.F.= balsam fir, W.S.= white spruce.

0.85% dw (1982) and mean total sugar values of 3.5% dw (1981) and 3.92% dw (1982) (Table 16). Mean sugar/nitrogen ratios were 4.84/1 in 1981 and 4.64/1 in 1982. White spruce trees in 1981 and 1982 had mean foliar nitrogen values of 1.24% dw (1981) and 1.20% dw (1982) and mean total sugar values of 3.32% dw (1981) and 3.67% dw (1982) (Table 16). Mean sugar/nitrogen ratios ranged from 2.7/1 in 1981 to 3.03/1 in 1982.

<u>Lower Michigan/Wisconsin</u>

Mean foliar nitrogen levels in balsam fir trees at Kellogg Forest, Michigan in 1983 and 1984 were 1.60% dw (1983) and 1.90% dw (1984) (Table 17). Mean total sugar values were 4.20% dw (1984) and 5.42% dw (1983), while mean sugar/nitrogen ratios were 2.32/1 in 1984 and 3.34/1 in 1983. Foliar nitrogen levels in Kellogg white spruce trees were 1.38% dw (1983) and 1.80% dw (1984) (Table 17). Mean total sugar values were 3.25% dw (1984) and 9.63% dw (1983), while mean sugar/nitrogen ratios ranged from 1.85/1 in 1984 to 6.95/1 in 1983. White spruce at Wellston, Michigan in 1984 had a mean foliar nitrogen value of 2.24% dw, mean total sugar value of 2.13% dw and a mean sugar/nitrogen ratio of 3.23/1 (Table 17). Balsam fir trees at Antigo, Wisconsin in 1984 had a mean nitrogen value of 2.84% dw, mean total sugar value of 6.86% dw and a mean sugar/nitrogen ratio of 2.6/1 (Table 17).

Insect Performance

Northern Minnesota

Insect performance clearly varied by host tree species. Performance variables which were measured included; combined male and female percent survival to the adult stage and male and female adult dry weight (Table 18). Balsam fir was by far the most suitable host with an overall grand mean female adult dry weight of 19.3 mg compared to 16.2 mg on white spruce and 10.6 mg on black spruce. Males showed the same pattern between species. There were little or no differences between years on the same host species, at least with respect to adult weight. This was not true for survival. For example, on balsam fir, survival ranged from a low of 12.4% (1984) to 30.4% (1981). On white spruce it ranged from a low of 21.3% (1981) to 34.9% (1982). On black spruce survival was 9.7% in 1981 but increased to 26.9% in 1982.

Lower Michigan/Wisconsin

Differences existing among host species from International Falls were not so evident from comparable field studies in Lower Michigan and Wisconsin (Tables 19, 20). Mean female and male weights on balsam fir were similar to those on white spruce. As before, there were no apparent differences between years on the same host species

Table 18. Grand mean values ± standard error for insect performance variables on a per tree basis. n= number of trees per study.

StudyArea/Yr/TreeSp.[2]	Performance Variables[1] % Surv	 Fwt	 Mwt
I.Falls 1981 B.F.	30.4±0.02 n=31	19.8±0.48 n=31	9.8±0.17 n=31
I.Falls 1982 B.F.	27.5±0.02 n=30	20.8±0.59 n=30	12.3±0.37 n=30
I.Falls 1981 W.S.	21.3±0.02 n=18	15.5±0.71 n=18	7.8±0.36 n=18
I.Falls 1982 W.S.	34.9±0.02 n=20	16.9±0.84 n=20	9.8±0.43 n=20
Cromwell 1981 Bk.S.	9.7±0.01 n=16	10.7±1.10 n=16	5.8±0.51 n=16
Cromwell 1982 Bk.S.	26.9±0.02 n=15	10.5±0.45 n=15	6.5±0.29 n=15

[1] % surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight.

[2] I.= International, B.F.= balsam fir, W.S.= white spruce, Bk.S.= black spruce

Table 19. Grand mean values ± standard error for insect performance variables on a per tree basis. n= number of trees per study.

	Study Area /year/tree species[1]			
Performance[2] Variables	Kellogg 83 B.F.	Kellogg 84 B.F.	I.Falls 84 B.F.	Antigo 84 B.F.
% Surv	24.8±0.02 n=20	37.7±0.02 n=34	12.4±0.02 n=11	19.3±0.01 n=28
Fwt	20.2±0.86 n=20	21.2±0.74 n=34	19.1±0.66 n=11	20.5±0.69 n=28
Mwt	10.4±0.40 n=20	10.6±0.23 n=34	10.0±0.48 n=11	10.7±0.27 n=28
Fagt	0.42±0.02 n=20	0.46±0.02 n=34	0.41±0.02 n=11	0.44±0.02 n=28
Magt	0.22±0.01 n=20	0.23±0.01 n=34	0.22±0.01 n=11	0.23±0.01 n=28
Fadt	2.09±0.02 n=20	2.17±0.01 n=34	2.15±0.02 n=11	2.15±0.01 n=28
Madt	2.13±0.02 n=20	2.19±0.01 n=34	2.16±0.01 n=11	2.17±0.01 n=28

[1] B.F.= balsam fir, I.= International

[2] % Surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight, fagt= female adult growth rate (mg/da), magt= male adult growth rate (mg/da), fadt= female adult development rate (%/da), madt= male adult development rate (%/da).

Table 20. Grand mean values + standard error for insect performance variables on a per tree basis. n= number of trees per study.

	Study Area /year/tree species[1]		
Performance Variables[2]	Kellogg 83 W.S.	Kellogg 84 W.S.	Wellston 84 W.S.
% Surv	26.8±0.02 n=33	43.5±0.02 n=32	47.4±0.02 n=34
Fwt	21.0±0.63 n=33	20.0±0.58 n=32	18.8±0.71 n=34
Mwt	11.5±0.32 n=33	10.1±0.23 n=32	10.0±0.27 n=34
Fagt	0.44±0.01 n=33	0.45±0.01 n=32	0.44±0.02 n=34
Magt	0.25±0.01 n=33	0.23±0.01 n=32	0.24±0.01 n=34
Fadt	2.09±0.01 n=33	2.24±0.01 n=32	2.32±0.01 n=34
Madt	2.16±0.01 n=33	2.23±0.01 n=32	2.35±0.01 n=34

[1] W.S.= white spruce

[2] % Surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight, fagt= female adult growth rate (mg/da), magt= male adult growth rate (mg/da), fadt= female adult development rate (%/da), madt= male adult development rate (%/da).

for adult weight. Survival, however, did vary between years. On balsam fir trees, it ranged from a low of 19.3% (1984 Antigo) to 37.7% (1984 Kellogg). On white spruce, survival ranged from a low of 26.8% (1983 Kellogg) to 47.4% (1984 Wellston).

Regression Relationships Between Insect Performance and Foliar Sugar and Nitrogen

Northern Minnesota

Foliar sugar and nitrogen levels apparently had little effect on tree to tree variation in budworm survival rates. Regression analyses indicated that in only two of six cases (Table 21) were either sugars (+G) or nitrogen (+Log N^2) linked to survival. Female weight was positively linked to nitrogen levels (N^2, LogN^2) in three of six cases and in one case to levels of glucose. Male weight was positively linked to nitrogen in one case (N^2, LogN^2) and to sugars (+F,-G,-S/N) in another.

Lower Michigan /Northern Wisconsin

As before, foliar sugar and nitrogen levels apparently had little effect on tree to tree variations in budworm survival. The regression analyses indicated that in only two of seven cases were either sugars (+G) or nitrogen (+LogN)

Table 21. Regression relationships between insect performance variables and selected host plant nutrients. (+) or (-) indicates significant ($p \leq .05$) positive or negative correlation coefficients.

	Performance Variables[1]		
StudyArea/Yr/TreeSp.[2]	% Surv	Fwt	Mwt
I.Falls 1981 B.F.		+LogN^2	+F-G-S/N
I.Falls 1982 B.F.	+LogN^2		
I.Falls 1981 W.S.	+G	+LogN^2	
I.Falls 1982 W.S.		+G	
Cromwell 1981 Bk.S.		+N^2	+N^2+LogN^2
Cromwell 1982 Bk.S.			

[1] % surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight, F= fructose, G= glucose, N= nitrogen, S= total sugar, S/N= sugar/nitrogen ratio

[2] (S)=small, (M)= medium and mature, I.= International, B.F.= balsam fir, W.S.= white spruce, Bk.S.= black spruce

linked to survival (Tables 22,23). Female weight was linked to sugars in two cases (+F, -S/N) while male weight was linked to sugars in three cases (+F, $+S^2$, -S/N). The mean number of days to adult eclosion for females was linked to either sugars ($+S^2$, -LogS) or nitrogen (-LogN, $-N^2$, $-LogN^2$) in four out of seven cases. Number of days to adult eclosion was positively linked to sugar in only one case ($+S^2$). Female adult growth rate was linked to sugars only (+F, -LogS)in three of seven cases while male adult growth rate was linked to sugars in four cases (+F, $-S^2$, -LogS) and to nitrogen in one case ($+N^2$). Female adult development rate was positively linked to nitrogen in two cases (+LogN, $+N^2$) and to sugars in two cases ($-S^2$, +LogS). Male adult development rate was positively linked to sugars in one case only ($-S^2$).

For both areas in which experiments using balsam fir were performed (Northern Minnesota and Lower Michigan/Wisconsin) there were no clear, consistant nitrogen and sugar effects on budworm performance between years. There were, however, some consistant patterns within a single year at one experimental site. For example, on balsam fir trees at Kellogg in 1984, sugar levels (fructose) showed a clear pattern of positive consistent linkage to budworm growth (male and female adult weight and male and female adult growth rates). The same was true on balsam fir trees at Antigo in 1984 where sugars (S^2, LogS) were consistently linked to rates of growth and development (male

Table 22. Regression relationships between insect performance variables and selected host plant nutrients. (+) or (-) indicates significant ($p \leq .05$) positive or negative correlation coefficients.

	Study Area /year/tree species[1]			
Performance Variables[2]	Kellogg 83 B.F.	Kellogg 84 B.F.	I.Falls 84 B.F.	Antigo 84 B.F.
% Surv	+LogN			
Fwt		+F		
Mwt		+F		
Fd	-LogN+F	$-\mathrm{LogN}^2$		$+S^2-\mathrm{LogS}$
Md				$+S^2$
Fagt		+F		
Magt		+F	$+N^2$	$-S^2$
Fadt	+LogN-F			$-S^2+\mathrm{LogS}$
Madt				$-S^2$

[1] B.F.= balsam fir, F= fructose, N= nitrogen, S= total sugar

[2] % Surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight, Fd= days to female adult development, Md= days to male adult development, fagt= female adult growth rate (mg/da), magt= male adult growth rate (mg/da), fadt= female adult development rate (%/da), madt= male adult development rate (%/da).

Table 23. Regression relationships between insect performance variables and selected host plants nutrients. (+) or (-) indicates significant ($p \leq .05$) positive or negative correlation coefficients.

	Study Area /year/tree species[1]		
Performance[2] Variables	Kellogg 83 W.S.	Kellogg 84 W.S.	Wellston 84 W.S.
% Surv			+G
Fwt			+F-S/N
Mwt	$+S^2$		+F-S/N
Fd		$-N^2$	
Md			
Fagt			+F-LogS
Magt	+F		+F-LogS
Fadt		$+N^2$	
Madt			

[1] W.S.= white spruce, F= fructose, N= nitrogen, G= glucose, S= total sugar, S/N= sugar/nitrogen ratios

[2] % Surv= combined male and female % survival to the adult stage, fwt= female adult dry weight, mwt= male adult dry weight, fd= days to female adult development, md= days to male adult development, fagt= female adult growth rate (mg/da), magt= male adult growth rate (mg/da), fadt= female adult development rate (%/da), madt= male adult development rate (%/da).

and female days to adult eclosion, male and female adult development rates and male adult growth rate). White spruce, like balsam fir, also showed no consistent nitrogen or sugar effects on budworm performance between years or study areas. There were, however, some consistent patterns within a year for the same experimental site. For example, on white spruce trees at Wellston in 1984, sugars (+F, +G, -LogS,) were linked to budworm growth and survival with five positive correlations (% survival, male and female adult weight and male and female adult growth rate) and two negative correlations (male and female adult growth rate).

Discussion

Diet Matrix Study

Quantities of soluble sugars and nitrogen as well as the relative proportions of these nutrients play important roles in the growth and development of the spruce budworm. This agrees in part with the work of Harvey (1974), who evaluated budworm performance on artificial diets with sugar/nitrogen ratios ranging from 1.10/1 to 8.82/1. He found that female spruce budworm pupal weight increased to a maximum (114.9, mg n=43) on diets containing roughly 4% nitrogen and a sugar/nitrogen ratio of 8.82/1. In the present study, maximum female pupal weight (106.2 mg, n=99 to 114.1 mg, n=128) occurred on diets containing 4.9%

nitrogen with sugar/nitrogen ratios between 1.31/1 and 2.61/1 (Figure 14). On diets containing one half the ammount of nitrogen (2.45%), maximum female pupal weight (105.0 n=53 to 107.0 n=91) occurred on a larger and broader sugar/nitrogen range (5.24/1 to 10.49/1) (Figure 14). Harvey (1974) further found that female larval survival to the pupal stage was positively correlated with increasing sugar/nitrogen ratios. He found that on diets containing 4% nitrogen, survival was poorest (29.6%) at a sugar/nitrogen ratio of 1.10/1 and highest (46.6%) at a ratio of 1.98/1. On diets containing 4.9% nitrogen in the present study, maximum male and female survival (72.0%) occurred at a sugar/nitrogen ratio of 2.61/1 whereas minimum survival (45.5%) occurred at a sugar/nitrogen ratio of 1.31/1 (Table 1 and Figure 1). On diets containing one half that amount of nitrogen (2.45%), maximum survival (52.2%) occurred at a ratio of 5.24/1 whereas minimum survival (24.5%) occurred at a ratio of 15.73/1 (Table 1 and Figure 1). Harvey (1974) also measured pupal development rate (%/da). He found that on diets containing 4% nitrogen, female pupal development rate generally increased with increasing sugar/nitrogen ratios. The slowest development (3.70%/da, n=15) occurred at a sugar/nitrogen ratio of 1.98/1 and fastest development (4.35%/da, n=43) at a sugar/nitrogen ratio of 8.82/1. The present study measured development rates for females on diets containing 4.9% nitrogen and found that slowest rates (3.18%/da, n=480, and n=162) occurred at two sugar/nitrogen ratios; 3.93/1 and 0.73/1 and fastest rates (3.47%/da, n=285) occurred at a ratio of 2.61/1 (Table 10 and Figure 10). On diets containing 2.45% nitrogen, the slowest development rate (2.45%/da, n=30) occurred at a sugar/nitrogen ratio of 15.73/1 and the fastest development rate (2.91%/da, n=43) at a ratio of 5.24/1.

Although the study of Harvey (1974) and the present study do not always agree on specific values, it is obvious that both studies demonstrate that there is an optimal sugar/nitrogen ratio, and that this optimal ratio seems to be most dependent upon the level of nitrogen in the diet.

The present study included experiments with diets containing 1.38% nitrogen, which had sugar/nitrogen ratios ranging from 2.59/1 (3.55% sugar) to 28.0/1 (38.46% sugar). Here, peak performance occurred across a broad sugar/nitrogen range, extending from 2.59/1 to 18.67/1. This probably occurred partly because of small sample sizes but also was due to the increased importance of soluble sugars at such low levels of nitrogen.

It should be pointed out that the low level nitrogen diets (1.38 and 2.45%) contained reduced levels of wheat germ, the source of the budworm's fattyacids. Commercial wheat germ is made up of approximately 10.8% lipid (Hlynka 1964). Roughly 84% of the fatty acids contained within this lipid portion are in the unsaturated form, mostly linoleic a, linoleic b and oleic acids. The major saturated fatty acids in wheat germ are palmitic and stearic acids. Most insects display an absolute requirement for polyunsaturated fatty acids whereas saturated and monosaturated fatty acids may be synthesized from non-lipid precursors (Downer 1978). To study the significance of this loss, I prepared two sets of diets containing 2.45% nitrogen to which fatty acids were applied. In these experiments one ml each of linoleic and linolenic acids or two mls of wheat germ oil were added to the casein portion of the diet media via an acetone solvent. Female pupal weights on diets containing added fatty acids or added wheat germ oil were significantly lower (Duncans multiple range test, ($p \leq .05$) than the equivalent diets containing no added oils (Table 15). Thus, it would seem that the reduction in fatty acids at the 2.45% level of nitrogen was not a significant factor affecting growth. Whether this reduction in fatty acids was in some way responsible for the poor response of the budworm at the lowest nitrogen level (1.38%) remains unknown from the results of this study.

In addition to fatty acids, wheat germ is also an important source of minerals for the budworm in artificial diets. Minerals such as mangenese, phosphorous and potassium at appropriate levels have positive effects on fecundity and growth (House 1965). Because minerals can be important in trace amounts, and are often present in trace amounts in various components of artificial diets, it is often very difficult to formulate diets of a known mineral content (Fraenkel 1958). Indeed, this was a problem in this study because in reducing nitrogen levels by manipulation of wheat germ content, mineral levels were also reduced. Whether this reduction in mineral levels was in some way responsible for the poor performance of the budworm at low nitrogen level diets (1.38) cannot be ascertained from the results of these experiments.

At the very highest sugar level (38.46%) budworm frass contained about 8% dw sugar, demonstrating that sugar levels were far beyond that which could be fully utilized (Figure 17). Increasing nitrogen while maintaining the same sugar level (38.46%), did not change the amount of sugars occurring in budworm frass. Sugars in frass were exclusively in the form of fructose and glucose whereas the diet contained almost exclusively sucrose (HPLC analysis). Thus it would seem to be a very costly process for spruce budworm to ingest and break down sucrose into its component parts and then not utilize them for energy. At sugar levels less than or equal to 25.64%, budworm frasscontained only 1% sugar or less at all nitrogen levels (Figure 17). Moreover, at levels less than or equal to 6.41% sugar at all nitrogen levels, frass contained virtually no soluble sugars at all. It appears then, that budworms can metabolize nearly all the sugars occurring in it's diet provided sugars do not exceed about 25% dw.

This study utilized diets containing 6.41% nitrogen in an effort to exceed the budworm's optimal level of dietary nitrogen. These diets had sugar/nitrogen ratios extending from 0.55/1 to 3.0/1. For most performance measures there were little or no differences between sugar levels. Most growth measurements were only slightly below values recorded on diets containing the next lowest level of dietary nitrogen (4.90%). Thus, it would seem that the budworm is generally less sensitive to the deleterious effects of supra optimal levels of dietary nitrogen compared to supra optimal levels of dietary sugar.

Albert et al. (1982) found that the behavioral threshold for sucrose was between 0.0001 and 0.001 M. My study utilized diets which had molar concentrations of sucrose well above this threshold (0.02 M, 3.55% sugar to 0.20 M, 38.46% sugar). Diets at sugar levels of 3.55 and 6.41% sugar (0.02 and 0.03 M) fell into the range of optimal feeding response (0.01 to 0.05 M; Albert et al. 1982). The remaining sugar levels; 12.80% (0.06 M), 19.23% (0.09M), 25.64% (0.12 M) and 38.46% (0.20M), exceeded the optimal range. The highest level of sugar (38.46%, 0.20 M) may in fact have served as a feeding deterrent rather than as a feeding stimulant.

Soluble sugars have been shown to be an important component of spruce budworm diet. Harvey (1974) reared budworm on artificial diets containing no soluble sugars and about 6.3% nitrogen. On these diets there were low pupal weights, long development times and poor survival (19%) although some were able to survive and lay fertile eggs. This study demonstrates that sugars become more important as nitrogen becomes limiting and that the budworm is generally far more sensitive to changing nitrogen levels than to changing sugar levels in artificial diets.

Field Studies

Balsam fir was the most suitable host plant in terms of budworm performance followed by white and black spruce. Mean nitrogen and sugar levels were not consistently different between species from year to year except for black spruce, which had consistantly low nitrogen levels. Mean foliar nitrogen levels were relatively uniform within species across all years. Mean total sugar levels, however, from balsam fir trees at International Falls, Minnesota increased yearly from 1981 (2.88%) to 1983 (8.12%) after which they declined slightly in 1984 (7.64%). The reasons for this upward trend are not known. However, it is of interest to note that mean rainfall recorded at the International Falls weather station for the 21 day period prior to foliage collection followed a similar upward trend (NOAA 1981-1984) and when regressed on mean total sugars showed a positive relationship (r^2=.91, significant at $p <.05$). Mean temperature for 21 days prior to foliage collection was variable between years and showed no significant ($p >.05$) trend. More work is needed, however, to determine if rainfall has an immediate effect on foliar sugar levels.

Balsam fir and white spruce foliar sugar and nitrogen levels varied considerably throughout the period of budworm larval development as well as from year to year. The ratios of these two nutrients were highly variable within and between years. The budworm must therefore be able to adjust to these changes during it's lifetime as well as from generation to generation.

Nitrogen and sugar effects did not appear to be consistantly related to budworm performance in the field studies. This may have occurred because the budworm can compensate for fairly wide variations in these nutrients so that their effects on budworm "fitness" are minimized. For example, larvae of other insects confronted with nutritionally poor foliage have been found to increase their rate of consumption or improve their digestive efficiency (Slansky and Scriber 1985). Conducting more field and laboratory studies such as those described in this thesis, along with studies of feeding behavior and digestive physiology would further clarify the relationships between this insect and it's host plants.

CONCLUSIONS

Diet Matrix Study

1. The optimal sugar/nitrogen ratio for all growth variables at every sugar and nitrogen level was 2.61/1 (4.90% nitrogen and 12.80% sugar)

2. The optimal ratio of dietary sugar/nitrogen varied according to the level of nitrogen in the diet, but generally increased when dietary levels of nitrogen were low. This demonstrated an increased importance of sugar when dietary nitrogen was low.

3. Supra optimal levels of dietary sugar (> 30% dw)were deleterious to spruce budworm growth and development.

4. Supra optimal levels of dietary nitrogen reduced growth slightly but were not as deleterious as supra optimal levels of sugar.

5. Reductions in fatty acid and mineral levels may be an important factor in the poor response of the budworm at the lowest level of nitrogen (1.38%).

Field Studies

1. Balsam fir was the most suitable host plant in terms of budworm performance followed by white and black spruce.

2. Levels of balsam fir and white spruce foliar sugar and nitrogen varied considerably throughout the life cycle of the budworm.

3. Levels of foliar sugar and nitrogen were variable from year to year and may have been dependent on such factors as precipitation and temperature.

4. The ratios of these two nutrients from year to year and within the same year were therefore highly dynamic. The budworm must be able to adjust and accomodate to such changes between and within generations.

5. Nitrogen and sugar effects did not appear to be consistantly related to budworm performance. This may be due to the fact that budworms may behaviorally or physiologically compensate for fairly wide variations in these nutrients so that their effect on budworm "fitness" is minimized.

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