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Host Preference and Nutrition Efficiency of the Gypsy Moth, *Lymantria dispar* L. (Lymantriidae: Lepidoptera), on Different Poplar Clones

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Abstract: Poplar is a tree species with a considerable growth rate and the ability to produce high yield in a short period of time, and is one of the main sources of wood in Iran. Considering its importance, the identification of poplar pests could have a significant effect on improving production and forest management. The gypsy moth, *Lymantria dispar* L. (Lymantriidae: Lepidoptera), is an important pest of forest trees in Guilan province, northern Iran. Therefore, host preference of this pest on the clones of *Populus deltoids* Bartram ex Marsh., *P. euramericana* (Dode), and *P. caspica* (Bornm.) was analyzed. The host preference of the pest was analyzed by olfactometric analysis, and the multiple choice method was also utilized to determine the rate of feeding and its effect on different clones. Some nutritional indices of 4th instar larvae, such as consumption rate (CR), frass production rate (FR), approximate digestibility of food (AD), growth rate (GR), and efficiency of conversion of ingested and digested food (ECI and ECD) were measured on these clones. The data obtained demonstrate that 4th instar larvae had the greatest host preference for *P. e. triple* ($P > 0.5$). Additionally, the lowest level of larval preference was for *P. caspica* and *P. d. 72/51* clones, as the highest feeding level was observed on *P. e. triple*. The results show that the local species *P. caspica* not only has low palatability for this pest, but also due to an interruption in larval food intake, low larval biological performance.

Key Words: Host preference, gypsy moth, *Lymantria dispar*, olfactometric analysis, *Populus* spp., poplar clones

Introduction

The ever increasing demand for wood and wood products, and decreases in forested areas in Iran have made the cultivation of fast growing trees the priority of forest management. Short-rotation woody crops (SRWC) are being developed as a sustainable system that simultaneously produces a renewable feedback for bioproducts, and a suite of environmental and rural development benefits (Nordman et al., 2005). In this regard, poplars with a high rate of biomass production are quite appealing as SRWC, although they can also be used for phytoremediation, carbon sequestration, and erosion control (Coyle et al., 2006).

An essential for biomass production in short rotation coppice systems is the stability of plantations against biotic factors. Considering entomological aspects, the risk of damage brought about by herbivorous insects must be minimized. In general, reduction of the leaf area by

defoliators or destabilization of shoots and stems by wood-boring insects may decrease growth and increase the risk that biomass production will fall below an economically acceptable level (Gruppe et al., 1999). Poplars, like any other plant, are not excluded from damage due to pests and pathogens, and are invaded by many pests throughout the year. Some defoliating insects, including the gypsy moth, *Lymantria dispar* (L.) (Lymantriidae: Lepidoptera), can significantly reduce biomass production and negatively impact its sustainability. The gypsy moth is one of the most important and dangerous herbivorous insects of deciduous trees throughout the northern hemisphere (Elkinton and Liebhold, 1990). More than 500 hosts belonging to different plant families have been reported for this insect, as the gypsy moth is highly polyphagous and is widely distribution through out the world (Barbosa and Capinera, 1977).

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Utilizing pest-resistant cultivars or a mixture of clones in integrated pest management is one of the best approaches for minimizing the damage caused by pests. Non-preference or host preference is a set of morphological and physiological factors, and chemical characteristics of the plant (Kogan and Ortman, 1978). Since susceptibility to insect damage varies widely among poplar clones, knowledge of their pest resistance can be used to make selections for breeding programs and large-scale deployment. Establishing large areas of SRWC with limited genetic diversity may increase the risk of catastrophic loss due to pests (Nordman et al., 2005). A major focus of *Populus* breeding programs is on producing high yielding genotypes; however, if not careful with selection schemes, there is the potential for the loss of pest resistance or tolerance if the breeding strategy focuses too narrowly on growth (Coyle et al., 2006).

Gansner and Herrick (1985) conducted a study on the defoliation intensity of the gypsy moth on several species of forest trees, including chestnut, black oak, elm, poplar, mulberry, beech, ash, and pine, in Pennsylvania. They reported that the preference was greatest for chestnut, moderate for poplar, mulberry and beech, and low for pine.

Many factors are involved in the host preference of gypsy moth larvae. Among the most important are plant species and regional plant diversity (Davidson et al., 2001), chemical composition of leaves (Foss and Riseke, 2003), and leaf age, which itself is the cause of physical and chemical changes (Meyer and Montgomery, 2004).

Different species of poplar in Iran have been previously studied in terms of their susceptibility and resistance to other pests (Salehi and Sadeghi, 2003; Haghghian et al., 2006), but studies are extremely limited regarding the host preference of the gypsy moth for different poplar clones. The objective of this study, therefore, was to investigate the host preference of the gypsy moth for 10 different poplar clones in northern Iran.

Materials and Methods

Determination of Host Preference

Gypsy moth eggs were collected in mid April 2007 from alder, poplar, and especially from ironwood with smooth stalks in the Guisom region of northern Iran, and then taken to the lab. The eggs were hatched at 25 ± 5 °C under a long-day photoperiod of 16 h L:8 h D.

The study included 5 *P. deltoides* clones (*P. d.* 72/51, *P. d.* 77/51, *P. d.* 73/51, *P. d.* 79/51, and *P. d.* 69/55), 4 *P. euramericana* clones (*P. e. triplo*, *P. e. castanzo*, *P. e.* 92/40, and *P. e.* 45/51), and an Iranian species, *P. caspica*.

To determine host preference olfactometric analysis was used. The olfactometer contained an insect maintaining store in the center and 10 leaf holding containers surrounding it. The containers were connected to the store by plastic tubes measuring 0.5 cm in diameter and 10 cm in length (Figure 1). In each experiment, only 1 leaf from each clone was placed in the containers and 4th instar larvae (n = 30) were placed in the center of the store. Five hours after the larvae were released the number of larvae feeding on the clones was counted. This was repeated 20 times to determine the percentage of preference of the larvae for the leaves of each clone.

To evaluate the host preference of 2nd and 4th instar larvae, another multiple-choice test was used. In this experiment we used a plastic tank containing water 15 cm deep. The tank was covered by aluminum foil and the circumference of the tank was immured with muslin. Then, the branches of 10 poplar clones were placed in the tank and 40 hungry larvae were released near the seedlings in each experiment. The larvae on each leaf were counted and the area of each leaf that was consumed was measured with a leaf area meter. Mean larval density on the clones was recorded on the basis of larval age and the area of each leaf that was consumed by larvae. In addition to these 2 methods, another experiment was used to determine the feeding rate of 2nd and 4th instar larvae during a known period (5 h). To do this, for each clone 30 similar plastic dishes were used and 1 poplar leaf was placed in each of them. After five 2nd and 4th instar larvae were placed in each dish they were covered by muslin to prevent the egression of larvae.

Determination of Nutritional Indices

In order to determine the 4th instars' nutritional efficiency, indices were calculated on a dry weight basis according to the procedures designed by Waldbauer (1968). The food consumption rate [CR = I / D.T] is the mean weight of dry food consumed per larva per day, where I is an index obtained by subtracting the oven dry

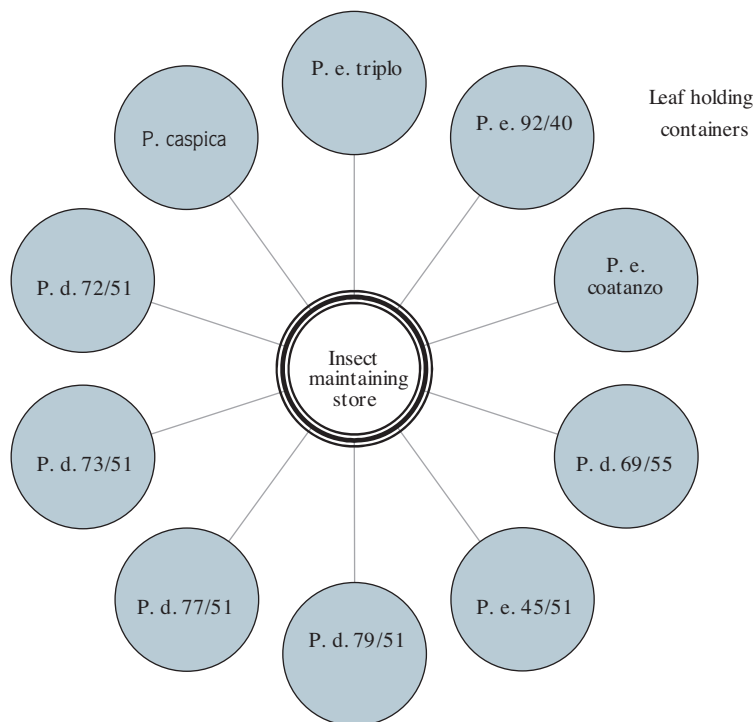


Figure 1. Schematic model of the olfactometric method.

weight of leaf fragments from the predicted oven dry weight of the remaining leaf and summing these differences over the entire feeding period; D is the density of larvae in each replication, and T is the eating period of the 4th instar larvae, which in the current experiment was 6 days. The frass production rate [$FR = F / D \cdot T$] is the mean dry weight of feces produced per larva per day. The approximate digestibility of food consumed [% AD = $100 (I - F) / I$] slightly underestimates the fraction of the ingested food that is assimilated. In the equation used to determine relative growth rate [$GR = G / W \cdot T$], G is fresh weight gain, G is the difference between the initial and final weights of larvae in each replication, and W is the mean weight at the end of the feeding period. Additionally, the efficiency of conversion of ingested food to body substance [% ECI = $100 G / I$] and the efficiency of conversion of digested food to body substance [% ECD = $100 G / (I - F)$] were measured.

Oven dry weights of the feces and the remaining leaf fragments were obtained by drying them at 95 °C for 24 h. To obtain dry weight of leaves before feeding, fresh leaves were used to calculate a regression relationship between oven dry weight as the dependent variable and fresh weight as the independent variable. The best

predictor of oven dried leaf weight (Y) was $Y = 2.588 X + 0.061$ ($R^2 = 0.91$), where X is fresh leaf weight.

Chemical and Physical Analysis of the Leaves

Leaves from all the poplar clones were collected during the experimental period in July 2007, dried in the shade, and prepared for chemical analysis. Total organic nitrogen content was determined by the micro-Kjeldahl method, potassium content was measured by flame photometry, using a lithium internal standard, and phosphorus content was determined using the Molybdate blue method at 470 nm, according to Bray and Kurtz (1945).

Moisture content of the leaves was determined using an automatic moisture analyzer. Evaluation of the leaf characteristics of each poplar clone was conducted by measuring leaf thickness and area.

Statistical Analysis

The data obtained in this research were analyzed utilizing the GLM function to obtain the least significant difference among the data. Significance was tested using Tukey's test at the 95% significance level. Statistical analyses were performed using SPSS v.10.0 for Windows (Statistical Package for Social Sciences (SPSS), Chicago, IL, USA).

Results

Host Preference

Tables 1 and 2 outline the data obtained from the host preference analysis of the gypsy moth for different poplar clones. The results show that *P. e. triplo* was the most preferred by gypsy moth larvae and the greatest damage was also observed to this clone ($P < 0.05$) (Table 1). The experiments based on olfactometry demonstrated that *P. caspica*, *P. d. 73/51*, and *P. d. 72/51* were preferred the least, while damage caused by larval feeding did vary considerably among *P. e. triplo*, *P. e. 92/40*, *P. e. costanzo*, and *P. d. 69/55* (Table 1). Based on the multiple-choice tests *P. e. triplo* and *P. e. 92/40* were the 2 clones most preferred by the gypsy moth larvae. The damage to *P. e. triplo* by 2nd instar larvae was about 0.56% according to this method, while 4th instar larvae caused 5.68% defoliation to this species. *P. caspica*, along with *P. d. 79/51*, *P. d. 77/51*, *P. d. 73/51*, and *P. d. 72/51* clones were preferred the least (Table 2).

Leaf area consumed by 4th instar larvae feeding on *P. e. triplo* and *P. caspica* varied considerably, ranging from about 15.5 mm² for the least preferred clones to 1189.8 mm² for the most preferred clones. Eating speed of the fasting larvae is another factor that was controlled by leaf

quality. Figure 2 shows the similarity of the rates of feeding for 2nd and 4th instar larvae on each of the poplar clones. Eating speed of the larvae was highest (16 mm² h⁻¹) on the leaves of *P. e. triplo* and lowest (4.66 mm² h⁻¹) on *P. caspica* (Figure 2).

Nutritional Indices

The data obtained demonstrated that CR, FR, and GR were at their highest levels when the larvae fed on *P. e. triplo* (Table 3). The CR and GR of larvae that fed on *P. e. 92/40*, *P. e. castanzo*, and *P. d. 69/55* clones were not significantly different from those that fed on *P. e. triplo*, but there was considerable difference among these larvae in the approximate digestibility rate; therefore, this index was highest for larvae that fed on *P. e. 45/41*. The larvae that fed on *P. e. triplo* had the highest CR and GR, but not the maximum AD in this experiment. Larvae that fed on *P. caspica* had the lowest values for these parameters. Although ECD varied among all the groups of larvae, from 59.02% for those that fed on *P. caspica* to 119.88% in larvae that fed on *P. e. 92/40*, the difference between them was not statistically significant. Nonetheless, ECI showed a direct relationship to CR and GR, and the highest ECI was recorded in larvae that fed on *P. e. triplo* (39.09%).

Table 1. Gypsy moth larvae host preference based on olfactometric analysis.

Poplar Clone	Leaf Area Consumed (mm ²)	Larval Damage (%)	Preference (%)
<i>P. e. triplo</i>	410.33 a	9.63 a	17.83 a
<i>P. e. 92/40</i>	289.66 ab	7.65 ab	14.41 b
<i>P. e. coatanzo</i>	247.16 abc	6.06 abc	13.31 bcd
<i>P. d. 69/55</i>	218.66 a-d	5.26 a-d	10.51 bcd
<i>P. e. 45/51</i>	85.50 bcd	2.01 bcd	6.65 bcd
<i>P. d. 79/51</i>	68.16 cd	1.66 cd	7.75 bcd
<i>P. d. 77/51</i>	58 cd	1.27 cd	4.43 cd
<i>P. d. 73/51</i>	14.16 d	0.31 d	1.10 d
<i>P. d. 72/51</i>	10.83 d	0.26 d	1.10 d
<i>P. caspica</i>	5 d	0.15 d	0.55 d
± SE	22.29	0.55	0.93
F	8.66	8.17	9.65

There is no significant difference between the numbers that are shown with the same letter in columns.

Table 2. Gypsy moth larvae host preference based on a multiple choice test.

Poplar Clone	2 nd Instar Larvae			4 th Instar Larvae		
	Leaf Area Consumed (mm ²)	Larval Damage (%)	Preference (%)	Leaf Area Consumed (mm ²)	Larval Damage (%)	Preference (%)
<i>P. e. triplo</i>	121.16 a	0.56 a	33.33 a	1189.8 a	5.68 a	25.41 a
<i>P. e. 92/40</i>	77.00 b	0.41 ab	22.91 ab	788.50 ab	4.35 ab	19.58 ab
<i>P. e. coatanzo</i>	14.83 d	0.07 cd	5.00 cd	659.83 b	3.33 ab	13.75 bc
<i>P. d. 69/55</i>	58.83 b	0.27 bc	14.58 bc	568.50 bc	2.70 ab	13.75 bc
<i>P. e. 45/51</i>	14.50 d	0.08 cd	5.00 cd	339.50 bcd	1.62 ab	7.91 cd
<i>P. d. 79/51</i>	13.83 d	0.06 cd	2.50 d	152.16 cd	3.18 ab	5.83 cd
<i>P. d. 77/51</i>	12.16 d	0.05 cd	3.33 d	172.50 cb	0.79 b	4.58 cd
<i>P. d. 73/51</i>	6.50 d	0.02 d	1.60 d	73.16 d	0.35 b	2.50 d
<i>P. d. 72/51</i>	8.00 d	0.03 d	2.50 d	32.50 d	0.48 b	2.91 d
<i>P. caspica</i>	1.50 d	-	0.41 d	15.50 d	0.07 b	0.83 d
± SE	5.59	0.275	1.52	56.11	0.37	1.17
F	18.38	15.15	21.38	15.91	3.74	14.92

There is no significant difference between the numbers that are shown with the same letter in columns.

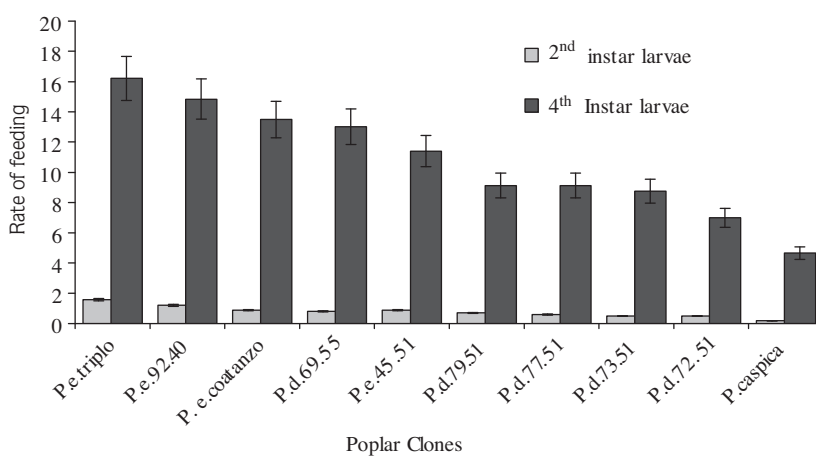


Figure 2. Feeding rate (mm² h⁻¹) of 2nd and 4th instar larvae on different poplar clones.

Poplar Leaf Chemical and Physical Analysis

The results of leaf analyses demonstrated that nitrogen content of the leaves was considerably different between the *Populus deltoides* and *P. euramericana* clones. *P. euramericana* clones had the highest nitrogen content levels. The highest nitrogen content was in the

leaves of *P. e. triplo* and *P. e. 92/40*, with 2.554% and 2.522% of leaf dry weight, respectively. It is obvious that high nitrogen content of leaves has a direct correlation with the level of protein. *P. caspica* had the lowest nitrogen content (1.66% of dry weight). This pattern was also observed for phosphorus and potassium.

Table 3. Some nutritional parameters of gypsy moth 4th instar larvae on different poplar clones.

Poplar clones	CR	FR	GR	AD	ECD	ECI
<i>P. e. triplo</i>	8.08 a	5.12 a	406.85 a	36.70 bcd	106.63 a	39.09 a
<i>P. e. 92/40</i>	7.55 ab	4.96 a	376.95 ab	34.73 cd	119.88 a	36.37 a
<i>P. e. coatanzo</i>	6.35 abcd	2.69 b	350.98 abc	57.63 ab	64.48 a	37.08 a
<i>P. d. 69/55</i>	6.46 abc	2.53 b	347.44 abc	60.81 a	59.31 a	35.91 a
<i>P. e. 45/51</i>	6.20 bcd	2.24 b	316.90 bcd	63.59 a	49.83 a	31.57 ab
<i>P. d. 79/51</i>	5.97 bcd	3.05 b	285.23 cde	48.03 abcd	61.80 a	28.49 abc
<i>P. d. 77/51</i>	5.98 bcd	2.57 b	264.80 de	56.99 abc	43.23 a	24.56 abc
<i>P. d. 73/51</i>	4.90 cd	2.46 b	237.63 ef	48.60 abcd	57.59 a	25.74 abc
<i>P. d. 72/51</i>	4.55 d	3.09 b	189.73 f	30.26 d	77.53 a	20.26 bc
<i>P. caspica</i>	2.48 e	1.74 b	96.06 g	29.11 d	59.02 a	16.38 c
± SE	0.29	0.21	17.02	2.58	5.96	1.56
F	17.86	15.97	43.6	8.54	2.52	7.06

There is no significant difference between the numbers that are shown with the same letter in columns.

CR: Consumption rate

AD: Approximate digestibility of food

FR: Frass production rate

ECD: Efficiency of conversion of digested food

GR: Growth rate

ECI: Efficiency of conversion of ingested food

Phosphorous content of the different clones varied from 0.253% to 0.41% and K content ranged from 0.575% to 1.5%. The *P. e. 45/51* clone had the highest phosphorous content; therefore, *P. euramericana* was preferred to a greater extent due to its higher nutrient content and ability to fulfill the nutritional needs of the larvae (Figure 3).

As is outlined in Table 4, leaf moisture was one of the most efficient parameters for food indices and for host preference by the gypsy moth larvae. Apart from the local variety, *P. caspica*, the leaves of *P. e. 45/51* clones had the highest moisture content and leaf thickness values (68.5% and 0.244 mm, respectively). The leaves of *P. deltoides* had the lowest moisture content and leaf thickness values. *P. caspica*, the local variety, had the lowest values for all the parameters (Table 4).

Discussion

With respect to the importance of poplar in SRWC, many studies have been conducted concerning the different effects of herbivores feeding on different species of *Populus*. Current research shows that gypsy moth larvae prefer some poplar clones to others, and

physicochemical characteristics of different leaves have a considerable effect, not only on the selection of the host by the pest, but also on feeding indices.

It was reported that the genetics of an individual clone is a key factor for determining its resistance to insect feeding (Nordman et al., 2005). In the present study most of the *P. euramericana* clones were highly susceptible to feeding by the insects. Many studies on the host preference of different pests on poplar clones confirm our recent findings (Nordman et al., 2005; Haghghian et al., 2006).

Gypsy moth larvae showed little preference towards the clones of *P. deltoides* and caused only minor damage in all the tests. The results also show that the highest density of gypsy moth larvae was on *P. euramericana triplo* leaves. These findings are in good agreement with many other studies conducted on a broad range of pests (Schevester et al., 1977, Salehi and Sadeghi, 2003, Haghghian et al., 2006). As such, it can be concluded that parentage plays an important role in group resistance to defoliation and most *P. deltoides* clones showed high resistance to gypsy moth larvae feeding (Coyle et al., 2006). Future research should include investigations on the various resistance mechanisms these clones possess.

Table 4. Some characteristics of poplar leaves.

Poplar Clones	Leaf Area (cm ²)	Leaf Thickness (mm)	Leaf Moisture (%)
<i>P. e. triplo</i>	226.2 b	0.239 b	64.71 b
<i>P. e. 92/40</i>	88.15 e	0.225 d	64.39 b
<i>P. e. coatanzo</i>	129.4 d	0.233 c	65.84 b
<i>P. d. 69/55</i>	221.5 b	0.241 ab	65.76 b
<i>P. e. 45/51</i>	228 b	0.244 a	68.65 a
<i>P. d. 79/51</i>	123.3 d	0.232 c	63.96 bc
<i>P. d. 77/51</i>	234.3 b	0.218 e	61.81 c
<i>P. d. 73/51</i>	306.4 a	0.221 e	63.89 bc
<i>P. d. 72/51</i>	175.4 c	0.218 e	61.94 c
<i>P. caspica</i>	55.39 f	0.211 f	54.18 d

There is no significant difference between the numbers that are shown with the same letter in columns.

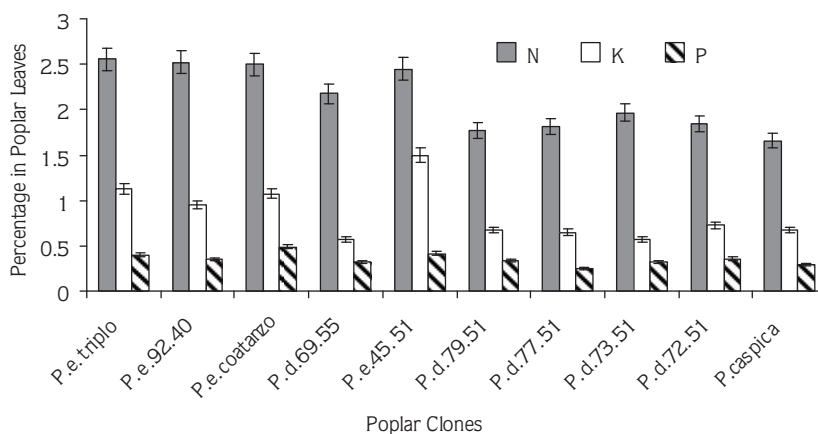


Figure 3. N, P, and K content of the leaves of different poplar clones.

Hwang and Lindorth (1997) demonstrated that variation in performance of gypsy moth and forest tent caterpillars proved to be strongly associated with genetically based variation in phenolic glycoside levels. It was reported that larvae reared on clones containing high concentrations of phenolic glycosides exhibited prolonged developmental time, and reduced pupal weight and fecundity (Osier et al., 2000). Moreover, for the gypsy moth there is an association between the occurrence of alkaloids and avoidance of certain tree species (Barbosa et al., 1990).

Few reports are available regarding variation in essential nutrient composition among *Populus* species and clones. Gruppe et al. (1999) demonstrated that the quantity of proteins and soluble carbohydrates could not explain the increased susceptibility of aspen, but they showed that the clones differed significantly in the amount of phenolic compounds, indicating good protection against herbivores due to high concentrations of tannins. Herbivore performance parameters were also positively related to foliar nitrogen concentration (Osier et al., 2000).

Rieske et al. (2002) showed that some nutrients, like carbohydrates with phagostimulatory characteristics, affected the feeding rate of gypsy moth larvae. The results obtained in the present study demonstrate that larval performance and nutritional indices improved when larvae fed on clones with *P. euramericana* parentage. According to Table 4 and Figure 2, the amount of nitrogen and moisture, and leaf thickness in these clones were considerably higher than in the others.

Leaf moisture and some nutritional contents, such as nitrogen, have an important role in larval feeding performance (Osier et al., 2000). Etebari et al. (2007) demonstrated that the level of nitrogen in an insect's diet had a direct effect on nutritional indices and that enrichment of the silkworm diet with some amino acids like glycine and glutamic acid increased the rate of consumption as well as the growth rate. Paul et al. (1992) showed that with an increase in leaf moisture content many feeding traits improved in Lepidopteran larvae, such that the food consumption rate, larval daily growth rate, digestion coefficient, and ingestion of food increased considerably. Because moisture content of leaves was one of the important factors that affected the feeding ability and ingestion of nutrients by the larvae, our current results confirm previous studies.

Differences in gypsy moth larval GR were expected among those feeding on different clones. *P. e. triplo* is preferred by the gypsy moth as a host plant, which helps to accelerate larval development and reduce the impact of natural enemies and other mortality factors, generally considered competitive advantages for insects (Price, 1997).

High ECI and CR rates are an indication the larval feeding has improved, resulting in larger larvae. Consequently, larger pupae are produced, which has a direct relationship to adult fertility and it is ecologically very important for the survival of this insect.

It was suggested that a combination of foliar characteristics may be responsible for insect preference and performance, and that an optimal combination of

foliar components serves to maximize host suitability (Foss and Rieske, 2003).

The present study observed a correlation between resistance and growth characteristics among the different poplar clones. Clones that did not have appropriate growth and had lower growth characteristics showed better resistance to the pests. *P. caspica* had the lowest growth indices, but were very resistant to the insects. This relationship has been observed in previous studies (Salehi and Sadeghi, 2003; Coyle et al., 2006).

Hwang and Lindorth (1997) observed a negative genetic correlation between growth and defense among aspen clones. Such information is critical for improving our understanding of the evolution of plant chemical defense systems. Genetic trade-offs may be especially common in species such as aspen, which are characterized by substantial genetic variation and show a capacity for both rapid growth and significant allocation to defense (Hwang and Lindorth, 1997).

In conclusion, herbivore host acceptance and suitability is a complex process that depends on physiological aspects of the herbivore, as well as the physical and chemical characteristics of the potential host (Foss and Rieske, 2003). Pest susceptibility, survival, and growth of different poplar clones have been previously monitored. With respect to group resistance in some poplar clones it is necessary that future screening focus on identifying leaf traits that confer broad-range insect resistance. Moreover, several variables must be taken into consideration when evaluating and selecting *Populus* clones for further testing or deployment. Ultimately, we must consider different factors when recommending clones for large scale cultivation, considering that the use of mixed clones is one of the best ways to suppress pest density.

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