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Seasonal Changes in Chemical Composition of Eurasian Watermilfoil (*Myriophyllum spicatum* L.) and Water Temperature at Two Sites in Northern California: Implications for Herbivory

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ABSTRACT

We compared seasonal changes in Eurasian watermilfoil (*Myriophyllum spicatum* L.) characteristics and water temperature for a shallow pond in Davis, CA, and the Truckee River, near Tahoe City, CA. Tissue C and N were 15% lower in plants from the Truckee River than in plants from the Davis pond. Seasonal fluctuations in tissue N were also different. Mean phenolic acid content of Truckee River plants (162 μM g^{-1}) was less than those from the shallow pond (195 μM g^{-1}). Phenolic acid content was positively related to tissue C for Truckee River and Davis pond plants and, tissue C:N ratio for Truckee River plants. Mean monthly water temperature (1990 to 1998) for the Truckee River site was less than 20 C. Water temperatures were warmer in August and September at this site. However, Eurasian watermilfoil collected during these months was characterized by lower levels of tissue N. During a 29-month period beginning January 1994, mean monthly water temperature for the Davis pond exceeded 20 C, only during July to September 1995. Tissue N was generally greater during summer for watermilfoil growing in the pond. These results imply that Eurasian watermilfoil biological control agents may have different developmental rates in these habitats, and thus different impacts on watermilfoil populations.

Key words: aquatic weed, tissue C, tissue N, phenolic acids, Truckee River

INTRODUCTION

Eurasian watermilfoil (*Myriophyllum spicatum* L.) is an important introduced aquatic weed in North America, where it is found from Florida to Quebec in the east, and California to British Columbia in the west (Couch and Nelson 1985). Its strong competitive abilities allow it to displace native species (Madsen et al. 1991), and its abundant biomass impedes water use for environmental, economic, and recreational purposes (Newroth 1985). Current management techniques include mechanical and chemical methods (Smith and Barko 1990). Recently, a native weevil *Euhrychiopsis lecontei* (Dietz), found in the northern U. S. and southern Canada, has been suggested as a possible biological control for this plant (Creed et al. 1992, Creed and Sheldon 1993, Creed and Sheldon 1994a,b, Creed and Sheldon 1995, Sheldon and Creed 1995, Newman et al. 1996, Creed 1998).

A number of factors influence the success of insects, employed as weed biological control agents, by regulating their abundance or the plant's response to them (Newman et al. 1998). Weather conditions and plant quality are two important factors among others (Newman et al. 1998). Temperature is an important factor in insect development. For example, *E. lecontei's* development time decreased as the temperature increased from 19 to 24 C (Newman et al. 1997). Plant quality also affects the herbivore's ability to persist and reproduce. Previous research with two insects (*Hydrellia pakistanae* and *Bagous hydrillae*) that feed on the submersed weed hydrilla, (*Hydrilla verticillata* (L.f.) Royle) showed that plant N content strongly influenced insect growth and development rates (Wheeler and Center 1996, Wheeler and Center 1997). This appears to be true for many additional weevil species as well (Cram 1965a,b, Hilliard and Keeley 1984a,b, Sands et al. 1983, Room et al. 1989, Hunt et al. 1993). Another aspect of plant quality that may influence the way herbivores or pathogens interact with a particular plant is the presence of defensive compounds, such as phenolic acids. Harrison and Durance (1989) point out that small increases in phenolic content of leaves can have large effects on potential consumers. For example, Geiselman and McConnell (1981) reported that feeding by *Littorina littorea* L. on two species of algae was reduced by more than 50% when the algal material contained 1% dry weight of phenols. When the phenolic content was increased to 2 to 5%, feeding was inhibited completely. There are also several examples of growth inhibition of microbes by phenolic compounds (Waterman and Mole 1994, Gross et al. 1996).

Eurasian watermilfoil occurs in California, but *E. lecontei* has not been reported from the state (Creed 1998). Therefore, the nature of the potential interaction between *E. lecontei* and Eurasian watermilfoil under California conditions is unknown. Additionally, most studies on the ecology of Eurasian watermilfoil have been conducted in the eastern U.S. (Grace and Wetzel 1978, Smith and Barko 1990). With the exception of work done in British Columbia (Newroth 1985) and Washington State (Perkins and Sytsma 1987, Getsinger

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et al. 1997), there is little published information on environmental conditions in western lakes and rivers inhabited by Eurasian watermilfoil. Thus, as a step toward evaluating the potential of *E. lecontei* as a biological control agent, we measured water temperature and plant characteristics (tissue C, tissue N, and total phenolic acid content) for Eurasian watermilfoil growing at two sites in northern California. Reported here are the results of those efforts.

MATERIALS AND METHODS

The two sites were a shallow pond located at the USDA-ARS Exotic and Invasive Weed Research Unit in Davis, CA, and a portion of the Truckee River between Tahoe City, CA and Alpine Meadows, CA, in the Sierra Nevada mountain range. Voucher specimens of plants from these sites have been deposited at the University of California, Davis herbarium.

At approximately two-week intervals, between May 1994 and June 1996 we collected plant samples from the Davis pond using a weed rake attached to a 6 m section of PVC pipe. The top 30-cm portions of 10 shoots were freeze-dried and the carbon (C) and nitrogen (N) content determined using a Perkin-Elmer model 2400 CHN analyzer with acetanilide used as the standard. Portions of shoot tissue were also analyzed for total phenolic acids as described by Hendry and Grime (1993). Water temperature and pH were measured at 0.5 h intervals with a datasonde (Hydrolab Corporation, Austin, TX) installed in the center of the pond. The pond was 10 m by 10 m. It had a trapezoidal cross section and was 1.5 m deep. Although we did not measure water column nutrient parameters during this study, the following values are typical during the summer: total inorganic P, 60 $\mu g\ l^{-1}$; NO_3-N, < 50 $\mu g\ l^{-1}$; NH_4-N, 80 to 120 $\mu g\ l^{-1}$ (R. Duvall, pers. comm.). During the course of this study, pH values measured with the datasonde ranged from 7.4 to 9.4. Groundwater, used to maintain the water level in the pond, has between 190 to 210 $mg\ l^{-1}$ total alkalinity.

Between May 1997 and October 1998 watermilfoil samples were collected at three sites in the Truckee River between Tahoe City and Alpine Meadows at approximately monthly intervals, except during periods when the area was inaccessible, due to snow accumulation. The sample sites were 0.3 km (site 1), 3.7 km (site 2), and 5.8 km (site 3) downstream from the river's origin at Lake Tahoe. Samples were collected by wading into the river and removing several shoots by hand at each site. Thus these samples are from plants growing at < 1 m depth. Plant samples were analyzed as described above. Water temperature data for the period 1990 to 1998 were obtained from the U. S. Geological Survey monitoring site at Tahoe City, CA. This data set consists of measurements made once a month on various days between 8 AM to 12 PM.

Due to the proximity of the sample sites to the outflow of Lake Tahoe, water quality in this section of the Truckee River is strongly influenced by characteristics of epilimnetic water in oligotrophic Lake Tahoe. Goldman and Horne (1983) reported that levels of inorganic P in Lake Tahoe surface water were typically around 2 $\mu g\ l^{-1}$ in summer or winter. They also reported that at 3 km downstream from its origin, Truckee River water NO_3-N levels were 20 $\mu g\ l^{-1}$ in summer, while NH_4-N was < 10 $\mu g\ l^{-1}$ in summer or winter. Goldman and Horne (1983) also reported levels of some minor and trace elements for Truckee River water. Fox (1982), using data from 140 samples collected at sites in the upper 22 km of the river from January, 1968 to December, 1980, estimated alkalinity to be 48.4 $mg\ l^{-1}$ in non-drought years. Measurements of pH from Fox (1982) taken in the portion of the river above our site 3 were between 7.0 and 7.8. Flow varies considerably with season, in a typical water year the mean flow at Tahoe City is 8 $m^3\ s^{-1}$ and legal agreements require that a minimum flow of 1.9 to 2.6 $m^3\ s^{-1}$ be maintained below the dam at Tahoe City, CA.

Elementary statistics for tissue C, tissue N, and total phenolic acid content were calculated (SAS Institute Inc. 1985). Linear regression equations relating phenolic acid content to tissue C, tissue N, or tissue C:N ratio were calculated using normal least-squares procedures following Draper and Smith (1981). We estimated degree-days for both the pond and river data sets using the averaging method as described in Zalom et al. (1983). In this method the lower threshold temperature is subtracted from the daily average temperature to yield the number of degree-days for each day. This method does not incorporate an upper threshold temperature and thus may overestimate degree-days on unusually warm days.

RESULTS AND DISCUSSION

Mean monthly water temperature for the Truckee River site was less than 20 C for the eight-year data set; warmest water temperatures occurred in August and September (Figure 1). Using this data set we estimated accumulated degree-days for the Truckee River. Given the 309 degree-day requirement for development from egg to adult for the watermilfoil weevil (Mazzei et al. 1999), the data indicate that if temperature is assumed to be the limiting factor, then just over two generations of weevils would be able to develop in the Truckee River. During a 29-month period beginning January 1994, mean monthly water temperature for the Davis pond exceeded 20 C only during July and August (Figure 1). However, because the water in the pond warmed earlier in the year, the number of accumulated degree-days was considerably greater in this habitat. From three to six generations of weevils should be able to develop at this site depending on year-to-year variation in temperature. Temperature differences for the pond and river sites imply that the potential biological control agent, the watermilfoil weevil, may have different developmental rates in these habitats.

Mean tissue C, over all samples, was higher for plants from the Davis pond than for plants from the Truckee River (Table 1). Tissue C fluctuated measurably through time in both the pond and river populations and discernible patterns were difficult to identify. In the Davis pond, Eurasian watermilfoil tissue C was lowest during late May, late July, and late September (Figure 2). Tissue C for Truckee River plants was lowest in December 1997 and May 1998 (Figure 3).

Patterns of seasonal change in tissue C were not as clear as those reported for total nonstructural carbohydrates in upper stems of a southern population of Eurasian watermilfoil (Madsen 1997). However, Madsen (1997) reported that low levels of stored carbohydrates occurred in July, April, and May over the three-year period of his study. He also reported that a secondary low level of carbohydrates occurred in October for all three years and noted the absence of this secondary low point for northern populations of Eurasian

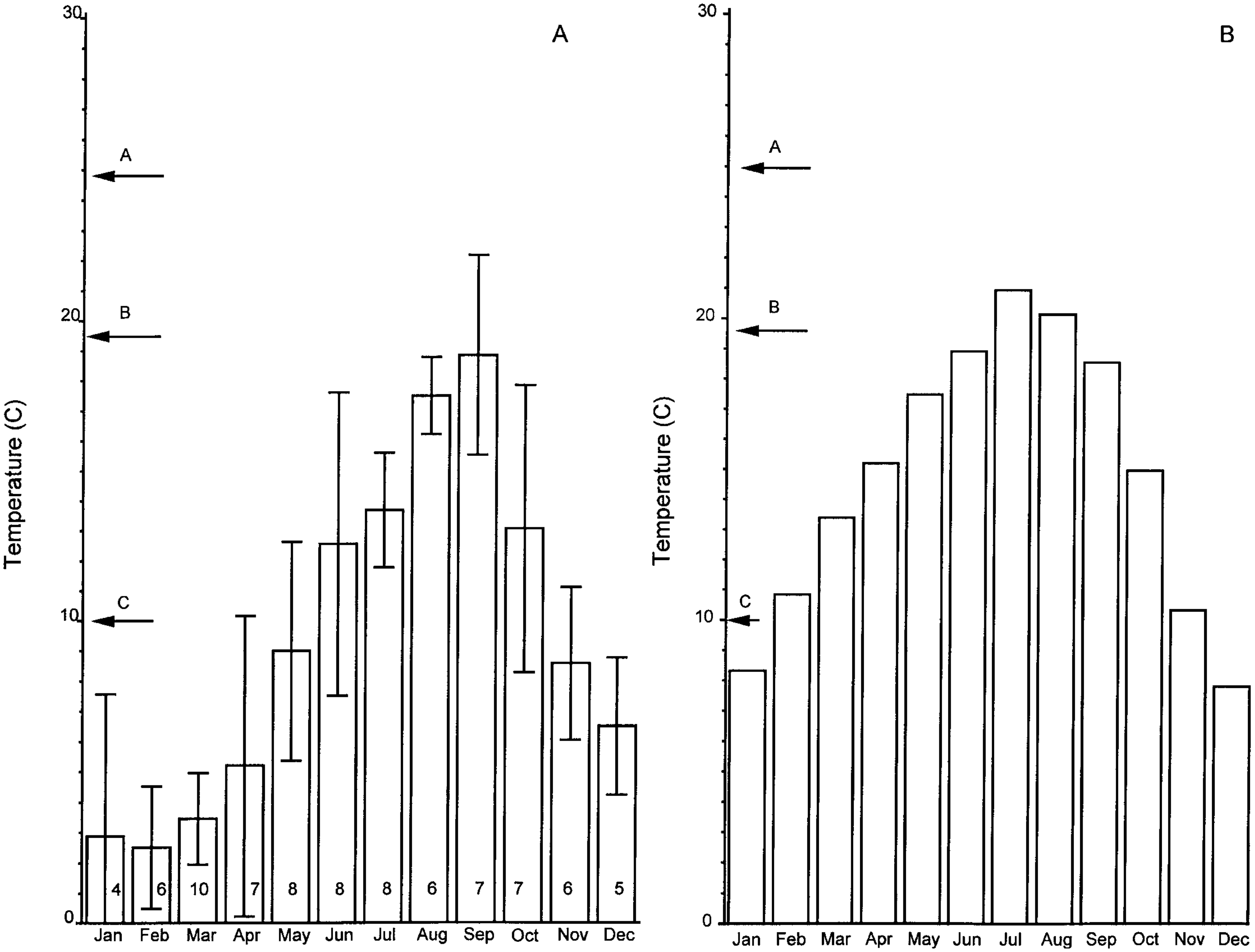

Figure 1. Mean monthly water temperature (and 95% confidence limits) for the Truckee River (A) and the Davis pond (B). Confidence limits not shown for Davis pond because they did not exceed line width of bar. Arrows indicate *E. lecontei* development times of 23 to 24 days at A, 38 to 41 days at B, and the developmental threshold (C), (Newman et al. 1997).

watermilfoil. In this respect, the September low points in tissue C observed in the Davis plants suggests that this aspect of the phenology of the Davis plants was similar to that of the southern population studied by Madsen (1997). Conversely, the pattern of tissue C for Truckee River plants more closely resembled patterns reported for northern populations of Eurasian watermilfoil (Madsen 1997).

Overall mean tissue N was 15% lower for plants growing in the Truckee River than for those growing in the Davis pond (Table 1). Seventy -five percent of all tissue N measurements were less than 2.43% for the pond population and less than 2.04% for Truckee River plants. Some tissue N values for plants from the Davis pond and Truckee River were within or below the range reported by Grace and Wetzel (1978), for Eurasian watermilfoil (1.40% to 6.29%).

Patterns of seasonal fluctuation in tissue N were also different for plants from the two sites (Figures 2 and 3). For Davis plants, tissue N was highest from January through March, declined to its lowest point in April through June, and increased slightly during summer (Figure 2). Tissue N for Truckee River plants was greatest in spring/early summer and declined sharply in late summer (Figure 3). Compared to Truckee River plants, tissue N was generally greater during summer for watermilfoil growing in the Davis pond. The pattern of tissue N for plants from the Truckee River was similar to that reported for plants from a Wisconsin lake. Carpenter and Adams (1977) measured tissue N for Eurasian watermilfoil at 13 sites in Lake Wingra between May and September 1975. They reported that tissue N was high in May and subsequently decreased and remained relatively constant during the rest of the growing season. In contrast, the Davis pond plants displayed two peak tissue N concentrations, one January through March, and a second during late summer.

Based on published results with another aquatic weevil, the differences in tissue N for milfoil growing in the pond and river would very likely contribute to different weevil development rates at the two sites. For example, a weevil that feeds on hydrilla increased its relative growth rate by 50%

Table 1. Tissue C (%), tissue N (%) and total phenolic acid content (μM g^{-1}) for two populations of Eurasian watermilfoil growing at two sites in northern California.

Parameter	C (%)		N (%)		Phenolic Acid (μM g^{-1})	
	Truckee River	Davis Pond	Truckee River	Davis Pond	Truckee River	Davis Pond
Number of Samples	140	777	140	777	140	777
Mean	33.00	38.02	1.78	2.10	162.3	194.5
Lower 95% CL	32.10	37.81	1.70	2.06	145.4	186.1
Upper 95% CL	33.90	38.24	1.85	2.14	179.2	202.9
Std. Deviation	5.14	3.02	0.45	0.54	101.4	119.2
Maximum	40.92	43.13	3.74	4.53	379.0	713.5
Minimum	18.45	19.54	0.74	0.7	2.3	17.6
75% Quantile	36.72	39.70	2.04	2.43	235.8	223.4
Median	34.61	38.20	1.77	2.00	161.5	138.4
Mode	25.72	36.53	1.77	1.66	33.3	23.6
25% Quantile	30.93	36.36	1.45	1.66	69.5	83.9

when fed plant material with 3.5% N versus plant material with 2% N (Wheeler and Center 1997). Since mean tissue N for the Davis plants was only slightly above 2%, weevils might not be expected to develop at the maximum rate in the pond, even though the thermal environment is favorable. Similarly, weevil development in the Truckee River might be expected to be lower than the maximum rate and might even be less due to a combination of low temperatures and low levels of tissue N in resident Eurasian watermilfoil plants.

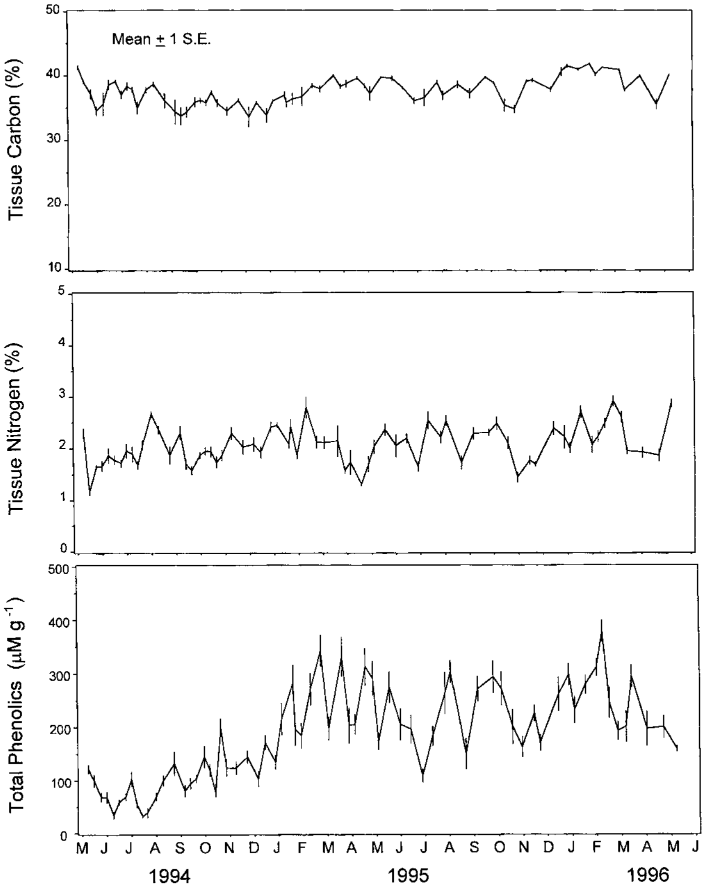

Figure 2. Phenolic acid content (μM g^{-1}), tissue N (%), and tissue C (%) for Eurasian watermilfoil in the Davis pond during 1994 to 1996. Error bars represent plus or minus 1 standard error, n = 10.

Phenolic acid content of Truckee River plants was less than for those from the pond (Table 1). For Davis plants, phenolic acid content was greatest during the winter (November through March) and was considerably less during the rest of the year (Figure 2). Phenolic acid content of Davis plants was positively related to tissue C and tissue N, but not tissue C:N ratio (Table 2). Seasonal changes in phenolic acid levels for Truckee River plants were different. Phenolic acid content was lower in December than at other times during the year (Figure 3). Even so, phenolic acid content increased at higher levels of tissue C or at higher tissue C:N ratios, but not tissue N (Table 2)

Phenolic acids may serve as defense against attack by herbivores or microbes. The levels of phenolic acids reported here are less than those reported for Eurasian watermilfoil by Planas et al. (1981). Planas et al. (1981) found a mean phenolic content of 7% and a maximum of 30% for Eurasian watermilfoil grown in laboratory cultures. Gross et al. (1996) reported total phenolic acid content of about 10% for Eurasian watermilfoil collected throughout the summers of 1991 to 1994 from a mesotrophic lake in northern Germany. When converted to percent of dry weight, the mean values reported here were 1.79% and 2.11% for watermilfoil from the Truckee River and Davis pond, respectively. Likewise, the maximum values were 4.26% and 8.99%, on a dry weight basis. During the growing season (April through September) phenolic acid content was similar in plants from both habitats. However, plants from the pond had higher levels during the winter than those in the Truckee River. This pattern differs somewhat from that reported for the marine macrophyte, eelgrass (*Zostera marina* L). Harrison and Durance (1989) examined seasonal variation in phenolic content of eelgrass shoots. They reported that the concentration of phenolic acids varied seasonally from a low in late winter/early summer of 0.65% dry weight to a high at the end of the active growing season of 1.54% dry weight.

Several factors cause variation in production of plant phenolic acids, among these is mineral nutrition. With respect to N nutrition, it has been generally observed that lower levels of phenolic acids are produced when the N supply is abundant (Waterman and Mole 1994). Thus, we would expect an

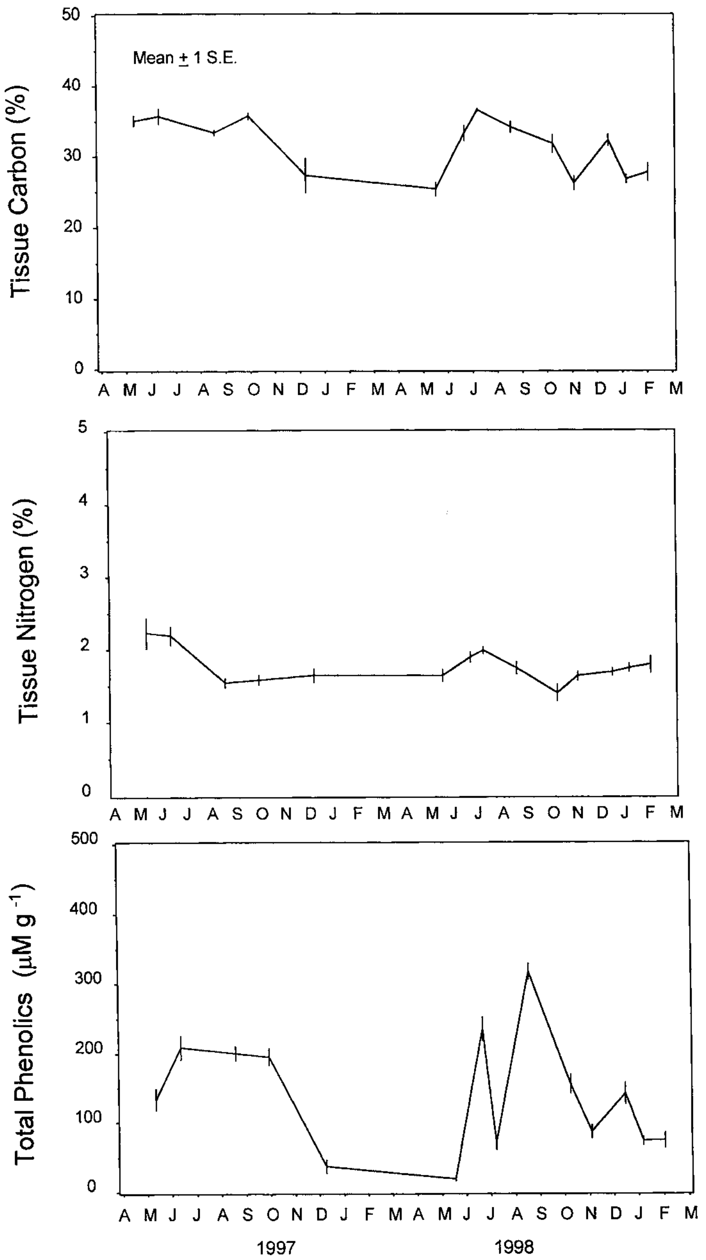

Figure 3. Phenolic acid content (µM g^{-1}), tissue N (%), and tissue C (%) for Eurasian watermilfoil in the Truckee River during 1997 and 1998. Error bars represent plus or minus 1 standard error, n = 15.

inverse relationship between phenolic acid content and tissue N. This was not the case for Eurasian watermilfoil from either the Davis pond or the Truckee River (Table 2). A second generalization that apparently holds true for Eurasian watermilfoil, at the sites examined here, is that phenolic acid content increases with increasing tissue C. A corollary observation is that at high C:N ratios phenolic acid content should increase (Waterman and Mole 1994). The significant positive relationships between phenolic acid content and tissue C agree with previously reported data from a variety of plants, but to our knowledge this is the first time such a relationship has been reported for Eurasian watermilfoil.

TABLE 2. REGRESSION EQUATIONS FOR PHENOLIC ACID CONTENT (µM G^{-1}) VERSUS TISSUE C (%), TISSUE N (%), OR TISSUE C:N RATIO. THE COLUMN LABELED "P" GIVES THE PROBABILITY OF A GREATER T-STATISTIC FOR A TEST OF THE NULL HYPOTHESIS THAT THE SLOPE EQUALS ZERO.

Site	Equation	R^2	P
Davis Pond	Phenolics = -275.91 + 12.37 C	0.10	0.001
Truckee River	Phenolics = -128.85 + 8.82 C	0.20	0.0001
Davis Pond	Phenolics = 122.43 + 34.32 N	0.03	0.001
Truckee River	Phenolics = 121.58 + 22.92 N	0.01	0.23
Davis Pond	Phenolics = 223.10 – 1.48 C:N	0.004	0.06
Truckee River	Phenolics = 63.2 + 5.10 C:N	0.06	0.005

The results of this study imply that the watermilfoil weevil should not be expected to have the same impact on watermilfoil populations at all sites in northern California because of differences in plant quality and water temperature. These results underscore the importance of understanding the relationship between Eurasian watermilfoil quality, water temperature, and development rate for the watermilfoil weevil. The information from this study can be used to design ecologically realistic experiments for assessing this relationship. Additionally, these data indicate that Eurasian watermilfoil growing in high light environments, with abundant photosynthate, may be better able to defend against herbivore or microbial attack due to higher levels of phenolic acids.

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