

Effects of agriculture on the abundance and community structure of epilithic algae in mountain streams of subtropical Taiwan

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ABSTRACT. This study aimed to characterize the abundance and community structure of epilithic algae and to examine the effects of intensive agriculture in mountain streams of the Wuling area. There were significant seasonal variations in epilithic algal biomass, with higher values in spring and winter and lower values in summer and fall. Effects of agriculture on the subtropical streams of the Wuling area were significant and varied with the extent of agriculture in the catchment. The biomass was significantly higher in Yousheng Stream with a larger area of agriculture than in other streams. Diatoms were the most abundant species, contributing over 85% to the total cell number. Most of these were pennatae diatoms, of which the genus *Achnantheidium* was the most abundant in the area. However, the communities showed clear seasonal and spatial changes. BIOENV analysis suggested that the combination of water temperature, conductivity, NO_2+NO_3 and SiO_2 concentrations and current velocity comprised the major factors explaining seasonal changes in the community, while the combination of NO_2+NO_3 and SiO_2 concentration and grazer density comprised the major factors affecting spatial changes. Changes in abundance and community structure of epilithic algae can be used to monitor the effects of agriculture in tropical/subtropical mountain streams.

Keywords: *Achnantheidium*; Current velocity; Diatoms; Grazer density; NO_2+NO_3 ; Wuling.

INTRODUCTION

Agriculture in a particular catchment area is considered among the most-serious threats to the streams within that area (Squires and Saoud 1986; Johnson et al., 1997; Wilby et al., 1998). There are positive relationships between stream nutrient concentrations and the area under agriculture (Leland and Porter, 2000; Rhodes et al., 2001; Kao and Chiu, 2004; Inwood et al., 2005). Nutrient loading from agricultural land is 10-20 times the load from forested land (Rekolainen, 1989; Pekárová and Pekár, 1996). Agricultural runoff can lead to higher nutrient concentrations in nearby streams (Chételat et al., 1999; Pan et al., 1999; Dodds et al., 2002) and to an acceleration of eutrophication (Rekolainen, 1989; Soranno et al., 1996). Although eutrophic impacts are thought to be greater in the tropics than at higher latitudes (Downing et al., 1999), studies of how agriculture effects tropical/subtropical streams are still very scarce.

Attached algae are often regulated by a variety of factors, such as nutrients, discharge, current velocity, light, grazers, and water temperature (Rosemend et al., 1993; Pan et al., 1999; Soininen and Kõnönen, 2004). The

nutrient contents of attached algae often show a positive correlation with the percent of the catchment area altered by human activities (Ekholm et al., 2000; Rhodes et al., 2001). Higher water temperatures resulting from the removal of riparian vegetation will increase attached algae abundance (Dodds et al., 2002), which may be 2-4-times higher in clear-cut streams than at other sites (Hill and Knight, 1988; Kiffney and Bull, 2000). However, little is known about the response of attached algae to agricultural land use in tropical/subtropical streams.

In Taiwan, many catchments of mountain streams at >1,500 m elevation have been developed for farming fruits and vegetables. The Wuling area is located in the upstream reaches of the Dajia River of central Taiwan at about 1,800 m in elevation, comprising three third-order streams: Cijiawan Stream, Yousheng Stream and Gaoshan Stream (Figure 1). They are characterized by having short, straight, steep channels and are often influenced by fluctuations in precipitation and typhoons. The catchment of Gaoshan Stream is vegetated by natural forests. The catchments of the Cijiawan and Yousheng Streams have each been developed for agriculture, but it is more intensive in the catchment of Yousheng Stream. The Cijiawan and Gaoshan Streams are the only habitats of the endangered Taiwanese masu salmon (*Oncorhynchus masou formosanus*). An early warning system to indicate

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if the streams in the Wuling area are changing due to agriculture is required. Comparative studies of the three streams with their different degrees of local agriculture would be helpful in determining the effects of agriculture on tropical/subtropical streams. The aims of the present study were: (1) to characterize the biomass and community structure of epilithic algae in the streams of the Wuling area; (2) to examine the effects of agriculture on this biomass and community structure.

MATERIALS AND METHODS

Study sites

In total, twelve sites were sampled in the streams of the Wuling area (Figure 1). The stream beds contain abundant rocks, primarily deposited by the weathering of sandstone and slate. The mean water temperature was 12°C, ranging from 18°C in summer to 10°C in winter. Climatic data derived from a local weather station (Wuling) during 2003-2004 (Climatological Data Annual Report, Central Weather Bureau of Taiwan) showed that in the dry season of October-April, the mean monthly rainfall normally does not exceed 40 mm, and that in the wet season of May-September, the average monthly rainfall frequently exceeds 150 mm. The mean discharge in the dry season was 1.84-2.30 m³ s⁻¹ and in the wet season was 2.58-2.96 m³ s⁻¹ (Chung et al., 2008).

Gaoshan Stream is 10.6 km long with a mean gradient of 140 m/km and a catchment area of 40 km². The stream

bed is dominated by pebble (39%) and rubble (27%) in winter, but consists of a high proportion of boulders (44%) in summer (Yeh, 2006). This catchment is vegetated by natural forests, and no agriculture is present (Wang, 1989), so the stream is assumed to be in a pristine state. Cijiawan Stream is 15.3 km long with a mean gradient of 130 m/km and a catchment area of 76 km². The stream bed consists of a high proportion of pebble (42%) in winter, but is dominated by rubble (26%) and boulders (21%) in summer (Yeh, 2006). The upper reach of Cijiawan Stream is bordered by riparian forest, but the lower reach has been developed for agriculture, including an area of 104 ha of vegetables, apples, peaches, and pears. It is considered to be moderately influenced by agriculture. Yousheng Stream is 11.4 km long with a mean gradient of 68 m/km and a catchment area of 31 km². The substrate is dominated by gravel (39%) and pebble (39%) (Yeh, 2006). The entire reach with an area of 295 ha has been intensively developed for farming vegetables since the 1970s. The stream has been channelized, and the natural riparian vegetation has been almost completely removed. It is regarded as highly influenced by agriculture. Canopy cover was higher in the Gaoshan Stream (90%) and the upper reach of the Cijiawan Stream (86%), and it was lower in the lower reach of the Cijiawan (57%) and Yousheng Streams (50%).

Sample collection

Riffles are the major habitat in the streams of the Wuling area. Attached algae samples were collected monthly from randomly selected rocks ($n = 5$) in the riffle zone of streams at 7:00-10:00 am from March 2003 to March 2004. On each rock, a frame made of steel was used to define a sampling area of an algal patch of 12.5 cm², and four algal patches were scraped off a surface area of 50 cm² with a toothbrush. The scraped algae were then washed off the toothbrush and rocks with 50-100 mL of filtered stream water. In the laboratory, the algal samples were centrifuged for 10 min to concentrate them to 5 mL. A 3-mL subsample was extracted for chlorophyll *a* in 90% acetone (Lobban et al., 1988). The other 2-mL subsample was fixed in Lugol's solution for taxon identification.

The taxon was identified and counted using a light microscope of Differential Interference Contrast (Zeiss Axioplan 2). Filamentous algae such as *Oscillatoria* and *Cladophora* were counted in every cell with a hemocytometer. Diatom samples were further treated with H₂SO₄ and KNO₃ (Sabater et al., 1990) and mounted with Naphrax. At least 500 diatom valves were counted per sample. Identification was carried out according to Patrick and Reimer (1966), Patrick and Reimer (1975), Round et al. (1990), Vyverman (1991), Yamagishi (1992), Round and Bukhtiyarova (1996), and Krammer and Lange-Bertalot (1997).

On each sampling occasion, water temperature, pH, conductivity, turbidity, dissolved oxygen (DO), and current velocity of the stream were measured *in situ* with



Figure 1. Sampling sites and agricultural areas (black circles) in the streams of the Wuling area.

portable meters (YSI 6560 multiparameter monitoring sensors and Son Tek Flow Tracker Handheld ADV) at 7:00-10:00 am. Water samples for other chemical factors were immediately placed on ice in a cooler and brought back to the laboratory for analyses of nitrite (NO_2^-) and nitrate (NO_3^-), total phosphorus (TP), biological oxygen demand (BOD), and SiO_2 following the standard methods of APHA (Clesceri et al., 1998). Density of grazers including Ephemeroptera and Trichoptera was determined by collecting with Suber net sampler (30.5×30.5 cm) by Kuo and Chiu (2004; 2005).

Data analysis

Shannon-Weiner diversity indices (H') were calculated using natural logs as indices of epilithic algal communities. A two-way fixed ANOVA model was used to determine whether environmental factors, epilithic algal biomass in terms of chlorophyll *a* or Shannon-Weiner diversity indices significantly differed among study sites or among seasons. Before the analyses, values of chlorophyll *a* were log-transformed (Clarke and Warwick, 1994) to conform to normality and homogeneity of variance assumptions. If the results of the ANOVA indicated significant treatment effects at the 0.05 probability level (p), then Fisher's protected least significant difference (LSD) test was used to determine which means significantly differed. The relationships of abundance of the epilithic algal taxon with environmental variables were determined using Spearman rank correlations.

In order to reveal spatial and seasonal patterns of the epilithic algal community, species compositions were studied using multivariate analyses in the PRIMER (vers. 5.2) computer package (Clarke and Gorley, 2001). The Bray-Curtis coefficient was used to produce a similarity matrix of species composition between any two samples according to the cell number of each taxon. Cell numbers were log-transformed to reduce the weighting of the dominant taxon in the communities (Krebs, 1999). The similarity matrix was first classified by hierarchical agglomerative clustering using the unweighted pair group mean arithmetic (UPGMA) linking method, and it was then ordinated using non-metric multidimensional scaling (MDS) techniques. A two-way crossed ANOSIM (analysis of similarities) was used to determine whether the effects of site and season on the community structure were significant by comparing the observed statistic to its permutation distribution in the absence of differences (Clarke and Warwick, 1994). If the results indicated significance at the 0.05 probability level, pairwise comparisons and the Bonferroni correction for the significance level were used to determine which levels differed. Similarity of percentages (SIMPER) was employed to reveal the most-common taxon in replicate samples for each group. BIOENV was employed to reveal the most influential environmental variables affecting the structure of the epilithic algal community. BIOENV selects the most influential environmental variable subset

by maximizing the weighted Spearman rank correlation (ρ_w) between the similarity matrix of species composition and similarity matrices of a combination of environmental variables considered at steadily increasing levels of complexity.

RESULTS

Environmental variables

For each site, monthly samples were pooled into one sample. Classification and MDS ordination separated the epilithic algal communities into four regions (Figure 1), including region I of the upper reach of the Cijiawan Stream (site A), region II of the lower reach of the Cijiawan Stream (sites B-F), region III of the Gaoshan Stream (sites G-I), and region IV of the Yousheng Stream (sites J-L).

In the Wuling area, water temperature ranged between 5.1-18.5°C (Table 1). DO remained high ($> 6.8 \text{ mg L}^{-1}$), but turbidity ($< 0.68 \text{ NTU}$) and BOD ($< 2 \text{ mg L}^{-1}$) remained low in all regions. pH values and conductivity, respectively, averaged 8.3-8.5 and 152-239 $\mu\text{S cm}^{-1}$. Current velocity was high with an average of 33 -65 cm s^{-1} . Concentrations of SiO_2 and TP in the water column were low and remained 4.18-6.14 and 0.02-0.03 mg L^{-1} , respectively, in all regions. However, $\text{NO}_2 + \text{NO}_3$ concentrations corresponded well with the area of agriculture in the catchment of the streams. $\text{NO}_2 + \text{NO}_3$ concentrations were high in the lower reaches of the Cijiawan Stream and even higher in the Yousheng Stream. The mean $\text{NO}_2 + \text{NO}_3$ concentration reached 5.65 mg L^{-1} in the Yousheng Stream. Mean canopy cover was 50%-90%. Grazer density averaged 261-839 individual m^{-2} .

Water temperature, turbidity, conductivity, current velocity, and grazer density underwent significant seasonal and regional changes (Table 2). Water temperature was higher in summer (18.5°C) and lower in winter (5.1°C). It was higher in the Yousheng Stream which lacked a canopy due to the agricultural activity, and lower in the Gaoshan Stream which had a high canopy. Turbidity was higher in the Yousheng Stream and lower in the upper reach of the Cijiawan Stream. It was higher in spring and lower in fall. Yousheng Stream and the upper reach of the Cijiawan Stream possessed greater conductivity values than other regions. The greatest conductivity value was observed in winter when the discharge was small. Current velocity was fastest in Gaoshan Stream, followed by the lower reach of Cijiawan Stream and Yousheng Stream, and was slowest in the upper reach of Cijiawan Stream. It was faster in summer and fall and slower in winter and spring. Grazer density was greater in Cijiawan Stream and lower in Gaoshan Stream and Yousheng Stream. It was greater in fall and winter and lower in spring and summer.

Nutrient concentrations also showed significant seasonal and regional changes (Table 2). TP concentrations did not differ among the regions. Concentrations of $\text{NO}_2 + \text{NO}_3$ were higher in Yousheng Stream, and the

Table 1. Environmental variables and grazer density of the four regions collected from March 2003 to March 2004 in the Wuling area. Values are presented as the mean±SD with the range in parentheses.

Site group	I	II	III	IV
Water temperature (°C)	11.8±2.4 (7.4-15.5)	11.8±2.4 (5.1-16.5)	11.2±2.8 (5.1-15.2)	12.8±3.3 (8.0-18.5)
DO (mg/L)	9.8±1.2 (7.5-11.4)	9.9±1.4 (6.9-13.2)	10.3±1.2 (7.0-13.0)	10.1±1.2 (6.8-12.2)
Turbidity (NTU)	0.14±0.11 (0.01-0.35)	0.19±0.17 (0.01-0.67)	0.24±0.18 (0.01-0.62)	0.34±0.23 (0.02-0.68)
BOD (mg/L)	0.60±0.39 (0.03-1.40)	0.61±0.33 (0.00-1.32)	0.62±0.40 (0.05-1.70)	0.69±0.42 (0.01-1.59)
pH	8.5±0.3 (8.1-9.1)	8.3 ±0.3 (7.7-9.2)	8.3 ±0.2 (7.9 -8.9)	8.3±0.6 (7.1-9.1)
Conductivity (µS/cm)	233±45 (200-350)	152±36 (90-230)	152±27 (125-210)	239±72 (130-390)
Current velocity (cm/s)	33±15 (15-60)	55 ±29 (14 -123)	65±26 (55-122)	53 ±27 (16-94)
SiO ₂ (mg/L)	6.14±0.74 (5.00-7.01)	4.18±0.81 (2.70 - 6.43)	4.99±0.72 (3.66-6.61)	4.53±0.87 (2.80-6.04)
NO ₂ +NO ₃ (mg/L)	0.24±0.14 (0.11-0.62)	0.70±0.60 (0.10-2.91)	0.26±0.39 (0.04-2.22)	5.65±3.84 (0.26-18.66)
Total P (mg/L)	0.02±0.02 (0.00-0.06)	0.02±0.03 (0.00-0.17)	0.03±0.05 (0.00-0.19)	0.02±0.02 (0.00-0.11)
Grazer density (individual/m ²)	839±354 (191-1444)	743±417 (69-1794)	310±179 (152-739)	261±203 (54-680)

Region I: the upper reach of Cijiawan Stream, region II: the lower reach of Cijiawan Stream, region III: Gaoshan Stream and region IV: Yousheng Stream.

mean value was 6-8-times that of other regions. SiO₂ concentrations were higher in the upper reach of Cijiawan and Gaoshan Streams. In general, these nutrient concentrations were higher in summer and fall and lower in winter and spring.

Epilithic algal community and biomass

Diatoms were the most dominant taxa of the epilithic algal communities in the streams of the Wuling area. Of 114 taxa identified, 107 taxa were diatoms, followed by cyanobacteria and Chlorophyta. Diatoms contributed 85% of the total cell numbers of the algal communities. Most diatoms belonged to pennatae genera, and > 40%

of the genera were of *Achnantheidium*. *A. atomus*, *A. minutissimus*, and *Platessa hustedtii* were the most abundant species.

Samples from all study sites were also pooled into monthly samples of combined sites. Classification and MDS ordination of the cell number of each taxon of the communities separated the monthly samples into four seasonal categories (Figure 2). The winter category contained samples collected during the period of December 2003 to February 2004; the spring category comprised samples from March 2004 and March 2003; the summer category was from April 2003 to October 2003; and the fall category was from November 2003.

Table 2. Two-way ANOVA (site \times season) of environmental variables and grazer density collected from the four regions in different seasons in the Wuling area. If the results of the ANOVA indicated significant treatment effects at the 0.05 probability level (p), then Fisher's protected LSD test was used to determine which means significantly differed. Means with the same letter do not significantly differ.

Source	df	<i>F</i> value	Pr > <i>F</i>	
Water temperature				
Site	3	5.01	0.003	IV ^a I ^{ab} II ^{ab} III ^b
Season	3	69.95	< 0.001	Summer ^a Fall ^b Spring ^c Winter ^d
Site \times Season	9	0.85	0.575	
DO				
Site	3	1.01	0.389	
Season	3	0.35	0.790	
Site \times Season	9	1.90	0.057	
Turbidity				
Site	3	7.88	< 0.001	IV ^a III ^b II ^{bc} I ^c
Season	3	13.22	< 0.001	Spring ^a Winter ^b Summer ^b Fall ^c
Site \times Season	9	0.22	0.992	
BOD				
Site	3	0.38	0.764	
Season	3	0.77	0.514	
Site \times Season	9	0.66	0.742	
pH				
Site	3	0.69	0.560	
Season	3	2.63	0.053	
Site \times Season	9	0.37	0.946	
Conductivity				
Site	3	43.86	< 0.001	IV ^a I ^a II ^b III ^b
Season	3	7.70	< 0.001	Winter ^a Spring ^b Summer ^b Fall ^b
Site \times Season	9	1.13	0.348	
Current velocity				
Site	3	17.06	< 0.001	III ^a II ^b IV ^c I ^c
Season	3	9.22	< 0.001	Summer ^a Fall ^{ab} Winter ^{bc} Spring ^c
Site \times Season	9	1.27	0.260	
SiO ₂				
Site	3	45.00	< 0.001	I ^a III ^b IV ^c II ^d
Season	3	42.66	< 0.001	Fall ^a Summer ^a Spring ^b Winter ^c
Site \times Season	9	0.85	0.568	
NO ₂ +NO ₃				
Site	3	59.88	< 0.001	IV ^a II ^b III ^b I ^b
Season	3	4.48	0.005	Summer ^a Winter ^{ab} Spring ^b Fall ^b
Site \times Season	9	8.35	< 0.001	
TP				
Site	3	0.79	0.501	
Season	3	5.98	0.001	Fall ^a Summer ^a Winter ^b Spring ^b
Site \times Season	9	0.28	0.979	
Grazer density				
Site	3	22.33	< 0.001	I ^a II ^b III ^c IV ^c
Season	3	3.18	0.026	Fall ^a Winter ^{ab} Summer ^b Spring ^b
Site \times Season	9	0.73	0.682	

df = degree of freedom. Region I: the upper reach of Cijiawan Stream, region II: the lower reach of Cijiawan Stream, region III: Gaoshan Stream and region IV: Yousheng Stream.

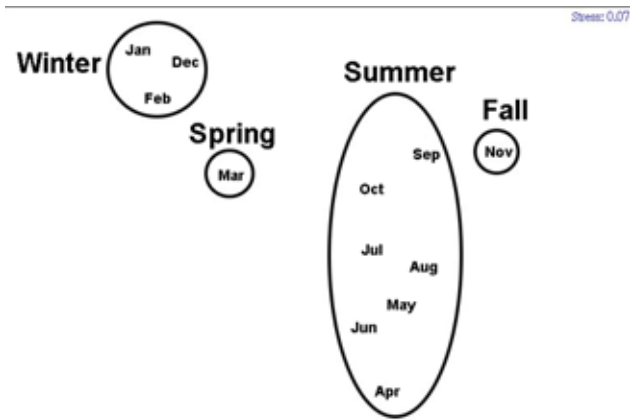


Figure 2. MDS ordination of Bray-Curtis similarities between epilithic algal communities collected monthly from March 2003 to March 2004 in the streams of the Wuling area.

The MDS ordination (stress = 0.07) revealed a clear and gradual seasonal shift in species composition from April 2003 to April 2004 in a counter-clockwise direction. There appeared to be a rapid shift in the epilithic algae communities from November (fall) to December (winter).

ANOSIM analysis demonstrated significant differences in epilithic algae communities among seasons ($R = 0.36$, $p = 0.001$). The pairwise comparisons further showed that the epilithic algae communities sampled in winter could be separated from those sampled in summer ($R = 0.55$, $p = 0.001$), fall ($R = 0.36$, $p = 0.001$), and spring ($R = 0.28$, $p = 0.001$).

The species richness of the epilithic algal communities was higher in Yousheng Stream, with its intense exposure to agricultural influences, than in other regions. Shannon-Wiener diversity indices of the epilithic algal communities revealed significant seasonal and regional differences. The Shannon-Weiner diversity indices were significantly higher in Yousheng Stream (1.85 ± 0.50) than in Gaoshan Stream (1.79 ± 0.36). The lower reach of Cijiawan Stream had the lowest diversity indices (1.62 ± 0.47). Diversity indices were significantly higher in fall (1.85 ± 0.41) and summer (1.79 ± 0.47) than in winter (1.70 ± 0.42) or spring (1.62 ± 0.47).

SIMPER analysis showed that mean similarity between any two regions was relatively lower in region IV (Yousheng Stream) with region I, II and III (Table 3). Region I (upper reach of Cijiawan Steam) and region II (lower reach of Cijiawan Steam) had a higher similarity.

Table 3. Mean similarity (%) of epilithic algal communities between any two regions of the streams in the Wuling area.

	I	II	III	IV
I	100	35.7	34.0	29.7
II		100	33.6	29.1
III			100	32.4
IV				100

The mean similarity between winter and other seasons was lower than that between other seasons and each other (Table 4). There was a relatively higher similarity between summer and fall. The mean similarity of the algal communities within each season was relatively lower in spring and higher in fall, indicating that the variability among replicated samples was greater in spring (Table 5). The seasonal shift in the epilithic algal communities in the Wuling area could be illustrated by changes in the relative abundances of the six most distinct taxa in each season, including the diatoms *A. atomus*, *A. minutissimum*, *P. hustedtii*, *Cocconeis placentula* and *Planothidium lanceolatum*, and the cyanobacteria *Oscillatoria* spp. *A. atomus* was the most frequently observed taxon year round, but it occurred more frequently in spring and less in fall. *P. hustedtii* also occurred year round, but was more frequently observed in fall and winter. *A. minutissimum* and *P. lanceolatum* also occurred year round, but showed unclear seasonal changes. *C. placentula* occurred more frequently in summer and fall, but disappeared in winter. The cyanobacteria including *Oscillatoria* spp., *Chroococcus* spp. and *Lyngbya* sp. and the chlorophyte *Cladophora* sp. also occurred more frequently in winter.

Achnantheidium, *Cocconeis*, and *Planothidium* were the most frequently observed genera of the epilithic algal communities in all of the regions examined in the Wuling area (Table 6). In the region I (upper reach of Cijiawan Steam), the two diatom genera *Cocconeis* and *Navicula* occurred more frequently than in other regions. The cyanobacteria *Chroococcus* spp., *Lyngbya* sp. and *Oscillatoria* spp. occurred more frequently in the region II (lower reach of Cijiawan Steam) than in other regions. In the region III (Gaoshan Stream), no cyanobacteria were observed, but *Gomphonema* was the most representative diatom genus. The diatoms *Cymbella cymbiformis* var. *nonpunctata*, *Cymbella* sp1., *Diatoma vulgaris*, *Encyonema minutum*, *Nitzschia sinuata* var. *tabellaria*, and *Nitzschia* sp1. occurred more frequently in Yousheng Stream than in other regions.

Epilithic algal biomass in terms of chlorophyll *a* also showed significant seasonal and regional differences (Figure 3). However, season and region showed a significant interaction. Chlorophyll *a* concentrations of epilithic algae collected from Yousheng Stream increased more rapidly and became greater in winter and spring, but no significant difference was detected from other regions in summer. Mean chlorophyll *a* concentrations of epilithic algae in Yousheng Stream reached 320 mg

Table 4. Mean similarity (%) of epilithic algal communities between any two seasons of the streams in the Wuling area.

	Spring	Summer	Fall	Winter
Spring	100	32.9	33.8	29.5
Summer		100	40.1	26.8
Fall			100	29.6
Winter				100

Table 5. Contribution (%) of species occurrence in seasonal epilithic algal communities in the streams of the Wuling area.

Season	Spring	Summer	Fall	Winter
Average similarity within each season	34.8	39.7	46.3	36.4
Species				
Bacillariophyta				
<i>Achnantheidium atomus</i> (Hust.) O. Monnier, Lange-Bert. Et Ector	22.1	15.5	14.2	16.9
<i>Achnantheidium minutissimum</i> (Kütz.) Czarn.	8.00	6.54	7.85	7.22
<i>Achnantheidium</i> sp.1	3.17	6.15	4.78	3.16
<i>Achnantheidium</i> sp.2		1.68		2.00
<i>Achnantheidium</i> sp.3		1.27	5.81	1.57
<i>Caloneis</i> sp.				10.7
<i>Cocconeis pediculus</i> Ehrenb. var. <i>pediculus</i>	5.17	1.62	2.55	1.45
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenb.) Grunow	6.10	15.6	13.8	
<i>Cymbella affinis</i> Kütz.				4.25
<i>Cymbella</i> sp.1	1.68			1.80
<i>Diatoma hyemalis</i> var. <i>mesodon</i> (Ehrenb.) Grunow	2.03	1.38		
<i>Gomphonema dichotomum</i> Kütz. var. <i>dichotomum</i>	1.11			
<i>Gomphonema minutum</i> (C. Agardh) C. Agardh	1.23	3.59		
<i>Gomphonema occultum</i> E. Reichardt & Lange-Bert.		1.24	1.66	
<i>Gomphonema olivaceum</i> (Hornem.) Bréb. var. <i>olivaceum</i>	1.70			
<i>Gomphonema tergestinum</i> Fricke var. <i>tergestinum</i>		2.68		
<i>Gomphonema</i> sp.2				1.63
<i>Navicula cryptocephala</i> Kütz.	1.08			
<i>Navicula</i> sp.1	2.58			
<i>Navicula</i> sp.2		1.97	1.37	
<i>Navicula</i> sp.4			2.11	
<i>Nitzschia sinuata</i> var. <i>tabellaria</i> (Grunow) Grunow			1.16	
<i>Nitzschia</i> sp.1			1.23	
<i>Planothidium lanceolatum</i> (Bréb. ex Kütz.) Round & Burkhtiy.	6.98	7.21	8.79	7.16
<i>Platessa hustedtii</i> (Krasske) Lange-Bert.	10.8	9.58	13.8	14.8
<i>Reimeria sinuata</i> (W. Greg.) J.P. Kociolek & Stoermer	1.49	3.6	3.46	
<i>Rossithidium pusillum</i> (Grunow) Round & Bukht.	3.74			1.40
<i>Synedra ungeriana</i> var. <i>pseudogaillonii</i> (H. Kobayasi et Idei)		1.25	3.86	
Chlorophyta				
<i>Cladophora</i> sp.				0.90
Cyanobacteria				
<i>Chroococcus</i> spp.	1.74	1.75		0.91
<i>Lyngbya</i> spp.	1.38	2.18		3.84
<i>Oscillatoria</i> spp.	7.11	5.27	3.93	8.41
Total	89.3	90.0	90.3	88.1

Table 6. Contribution (%) of species occurrence in regional epilithic algal community in the streams of the Wuling area.

Region	I	II	III	IV
Average similarity within each region	39.9	38.4	41.6	34.6
Species				
Bacillariophyta				
<i>Achnantheidium atomus</i> (Hust.) O. Monnier, Lange-Bert. Et Ector	16.1	18.2	17.6	15.5
<i>Achnantheidium minutissimum</i> (Kütz.) Czarn.	6.88	5.04	7.57	12.5
<i>Achnantheidium</i> sp.1	7.13	4.52	7.11	3.11
<i>Achnantheidium</i> sp.2			3.87	1.66
<i>Achnantheidium</i> sp.3	3.51	2.04		0.87
<i>Achnanthes</i> sp.1				2.38
<i>Caloneis</i> sp.		0.91		0.67
<i>Cocconeis pediculus</i> Ehrenb. var. <i>pediculus</i>	5.23	1.48	1.33	3.25
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenb.) Grunow	15.12	9.22	7.53	6.07
<i>Cymbella</i> sp.1				1.10
<i>Cymbella cymbiformis</i> var. <i>nonpunctata</i> Font.				0.91
<i>Diatoma hyemalis</i> var. <i>mesodon</i> (Ehrenb.) Grunow	2.64	1.01		0.60
<i>Diatoma vulgare</i> Bory var. <i>vulgare</i>				3.99
<i>Encyonema minutum</i> (Hilse ex Rab.) D.G. Mann				1.99
<i>Gomphonema dichotomum</i> Kütz var. <i>dichotomum</i>			1.80	
<i>Gomphonema minutum</i> (C. Agardh) C. Agardh		0.83	4.76	1.56
<i>Gomphonema occultum</i> E. Reichardt & Lange-Bert.			1.63	
<i>Gomphonema parvulum</i> (Kütz.) Kütz.			1.25	0.61
<i>Gomphonema tergestinum</i> Fricke var. <i>tergestinum</i>			3.40	1.73
<i>Gomphonema</i> sp.1			1.38	
<i>Navicula angusta</i> Grunow	1.44			0.98
<i>Navicula menisculus</i> Schum.	1.07			
<i>Navicula</i> sp.1	1.04			
<i>Navicula</i> sp.2	2.29	1.30	1.33	0.72
<i>Navicula</i> sp.3	0.97			
<i>Nitzschia sinuata</i> var. <i>tabellaria</i> (Grunow) Grunow				0.89
<i>Nitzschia</i> sp.2				1.75
<i>Planothidium lanceolatum</i> (Bréb. ex Kütz.) Round & Burkhtiy.	9.76	5.55	11.4	6.65
<i>Platessa hustedtii</i> (Krasske) Lange-Bert.	7.61	11.9	15.3	8.88
<i>Reimeria sinuata</i> (W. Greg.) J.P. Kociolek & Stoermer		2.48	1.25	2.08
<i>Rossithidium pusillum</i> (Grunow) Round & Bukht.			2.05	0.92
<i>Synedra ungeriana</i> var. <i>pseudogaillonii</i> (H. Kobayasi et Idei)	0.90	0.93		2.54
Cyanobacteria				
<i>Chroococcus</i> spp.		4.71		
<i>Lyngbya</i> spp.		5.70		
<i>Nostoc</i> spp.				0.93
<i>Oscillatoria</i> spp.	8.62	14.9		2.22
Total	90.3	90.7	90.5	87.1

Table 7. Spearman rank correlation coefficients between abundance of epilithic algal species and environmental variables in the streams of the Wuling area.

	Temperature	pH	Turbidity	Conductivity	NO ₂ +NO ₃	TP	SiO ₂	DO	Current velocity	BOD	Grazer density
<i>Bacillariophyta</i>											
<i>Achnanthyidium atomus</i> (Hust.) O. Momnier, Lange-Bert. Et Ector	-0.201*			0.264***	0.174*						-0.348***
<i>Achnanthyidium minutissimum</i> (Kütz.) Czarn.		0.197*	0.171*	0.373***	0.305***		0.177*		-0.158*		-0.346***
<i>Achnanthyidium</i> sp.1							0.237**				
<i>Achnanthyidium</i> sp.2											
<i>Achnanthyidium</i> sp.3											
<i>Achnanthes</i> sp.1		0.253**	-0.262***	0.324***	0.307***		0.157*		-0.289***		-0.313***
<i>Caloneis</i> sp.	-0.658***			0.293***		-0.243**	-0.534***		-0.242**		
<i>Cocconeis pediculus</i> Ehrenb. var. <i>pediculus</i>				0.160*					-0.314***		
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenb.) Grunow	0.529***		-0.264***	-0.261***	0.281***	0.527***				0.159*	
<i>Cymbella affinis</i> Kütz.	-0.526***			0.190*		-0.450***					
<i>Cymbella cymbiformis</i> var. <i>nopunctata</i> Font.	0.302***				0.158*	0.169*					
<i>Cymbella</i> sp.1	-0.463***		0.198*	0.326***	-0.295***	-0.374***			-0.199*	-0.218**	
<i>Diatoma hyemalis</i> var. <i>mesodon</i> (Ehrenb.) Grunow	0.171*			-0.264***		0.200*	-0.165*				
<i>Diatoma vulgare</i> Bory var. <i>vulgare</i>		0.202*	0.180*	0.455***	0.442***						-0.161*
<i>Encyonema minutum</i> (Hilse ex Rab.) D.G. Mann	0.344***		0.183*		0.320***						-0.229**
<i>Gomphonema dichotomum</i> Kütz var. <i>dichotomum</i>	0.164*			-0.165*		0.185*					-0.268***
<i>Gomphonema minutum</i> (C. Agardh) C. Agardh	0.341***			-0.168*		0.198*			0.231**		-0.320***
<i>Gomphonema occultum</i> E. Reichardt & Lange-Bert.			0.352***	0.314***							-0.175*
<i>Gomphonema olivaceum</i> (Homem.) Bréb. var. <i>olivaceum</i>			0.352***	0.314***							-0.290***
<i>Gomphonema parvulum</i> (Kütz.) Kütz.											-0.171*
<i>Gomphonema tergestinum</i> Fricke var. <i>tergestinum</i>	0.542***				0.179*	0.394***					-0.269***
<i>Gomphonema</i> sp.1	0.361***		-0.191*	-0.195*	0.181*	0.332***				0.213**	-0.182*
<i>Gomphonema</i> sp.2	-0.462***			0.201*		-0.373***					
<i>Navicula angusta</i> Grunow	0.206**					0.297***					
<i>Navicula cryptocephala</i> Kütz.					-0.166*						-0.186*
<i>Navicula meniscus</i> Schum.	0.319***		-0.199*	-0.224**		0.406***					
<i>Navicula</i> sp.1			0.171*		-0.231**						
<i>Navicula</i> sp.2			-0.181*	-0.178*		0.215**					
<i>Navicula</i> sp.4									-0.275***		
<i>Nitzschia sinuata</i> var. <i>tabellaria</i> (Grunow) Grunow	-0.164*	0.275***	0.170*	0.419***	0.227**	-0.191*			-0.216**		
<i>Nitzschia</i> sp.1	0.175*		-0.211**								

Table 7. (Continued)

	Temperature	pH	Turbidity	Conductivity	NO ₂ +NO ₃	TP	SiO ₂	DO	Current velocity	BOD	Grazer density
<i>Nitzschia</i> sp.2		0.163*		0.374***	0.387***						
<i>Planolthidium lanceolatum</i> (Bréb. ex Kütz.) Round & Burkhty.	-0.212**										-0.254**
<i>Platessa hustedtii</i> (Krasske) Lange-Bert.	-0.211**			0.221**				0.221**			
<i>Reimeria sinuata</i> (W. Greg.) J.P. Kociolek & Stoermer	0.314***		-0.165*		0.222**		0.176*				
<i>Rosstithidium pusillum</i> (Grunow) Round & Bukht.	-0.169*										-0.174*
<i>Synedra ungeriana</i> var. <i>pseudogaitlonii</i> (H. Kobayasi et Idei)	0.188*		-0.236**	0.206**	0.352**		0.178*			0.215**	
Chlorophyta											
<i>Cladophora</i> sp.	-0.227**			0.212**					-0.173*	-0.160*	
Cyanobacteria											
<i>Chroococcus</i> spp.						-0.157*					0.204*
<i>Lyngbya</i> spp.											
<i>Nostoc</i> spp.					0.193*						
<i>Oscillatoria</i> spp.	-0.213**						-0.288***				0.351***

*P<0.05; **P<0.01 and ***P<0.001.

agricultural fertilizers reached 59% of the total N load (Kunikane and Magara, 1984). The increases in NO₂+NO₃ concentrations are indicative of runoff from agriculture in the catchment. The NO₂+NO₃ concentration in Yousheng Stream is significantly higher than that of the Cijiawan and Gaoshan Streams, reflecting the high levels of fertilizers applied to agricultural land in comparison with other regions.

N, but not P, was found to stimulate attached algal production in subtropical streams with sufficient light (Mosisch et al., 2001). Filamentous green algae was also observed more frequently in open streams subject to high irradiance. Yousheng Stream basin had been clear cut, and the NO₂+NO₃ concentrations and chlorophyll *a* values significantly exceeded other regions. It thus had more filamentous green algae than other regions. Moreover, turbidity was also higher in Yousheng Stream and the lower reach of Cijiawan Stream. However, in Gaoshan Stream, bordered by riparian forests, NO₂+NO₃ concentrations and water temperatures remained low. Hill and Knight (1988) indicated that removal of riparian vegetation may change the amount of sunlight reaching the stream surface and thus the water temperature. In the upper Michigan River, forests were associated with lower stream NO₃ concentrations (Inwood et al., 2005). Our results suggest that clearing forests for agriculture in the catchment of subtropical streams not only increases NO₂+NO₃ concentrations, but also substantially increases erosion and sediment load from slope lands (Hornung and Newson, 1986) and water temperature.

Dissolved silicate in streams usually comes from mineral soils and bedrock, and the concentrations are higher in headwaters of the catchment. Detenbeck et al. (2003) indicated that SiO₂ concentrations in streams would decrease by reducing contact with mineral soils and bedrock in a stream system with high catchment storage, which is defined as the fraction of the catchment area covered by lakes and wetlands. In this study, we found that SiO₂ concentrations were lower in the agriculture-influenced Yousheng Stream and the lower reach of Cijiawan Stream. It appears that agriculture in the catchment reduced the inflow of dissolved silicate from mineral soils and bedrock into the streams. Dissolved silicate is known to be a main limiting factor for diatoms. In this study, we also found that almost all diatoms were positively correlated with SiO₂. Therefore, diatoms were relatively less abundant in the agriculturally-influenced regions and in winter and fall when the discharge and SiO₂ concentrations were lower in the Wuling area.

The tropical/subtropical monsoon climate in Taiwan is characterized by abundant rainfall in summer and dryness in winter. Streams of the Wuling area are thus dominated by flow regimes. Running waters in monsoon Asia often show distinct seasonality (Cusing et al., 1995). A lower stream discharge was found to result in greater attached algae biomass (Kishi et al., 2004). In mountain streams of the Wuling area, the discharge in the dry

season of October–April was $< 5 \text{ m}^3 \text{ s}^{-1}$, and the current velocity was relatively slow (15 cm s^{-1}). In the wet season of May–September, the discharge increased to $> 10 \text{ m}^3 \text{ s}^{-1}$, and the current velocity reached $> 60 \text{ cm s}^{-1}$. These facts might explain why cyanobacteria and chlorophytes were observed more frequently in winter when the current velocity was slower. Moreover, typhoons and thunderstorms often bring floods in summer. Consequently, the discharge became $20 \text{ m}^3 \text{ s}^{-1}$, and the current velocity reached 122 cm s^{-1} , which might have reset the attached algae communities to earlier successional stages (Oemke and Burton, 1986). The fast current velocity and changing flow regime have likely resulted in the dominance of small-sized diatoms such as *Achnanthes*, *Achnantheidium*, and *Cocconeis* in the streams especially in summer and fall. These small-sized diatoms are generally characterized by prostrate or crustose forms which tightly adhere to the substrate to resist detachment by flooding (Leland and Porter, 2000).

Despite this, classification and MDS ordination of the epilithic algal communities in streams of the Wuling area clearly reflected the effects of agriculture in the catchment. The epilithic algal communities were primarily affected by $\text{NO}_2 + \text{NO}_3$ concentrations in the streams resulting from agricultural runoff, and our conclusion is similar to the findings of Rosemond et al. (1993) and Dodds et al. (2002). High proportions and abundances of *A. minitissimum* were observed in association with extremely high $\text{NO}_2 + \text{NO}_3$ concentrations in Yousheng Stream. Correlation with environmental variables also showed that the presence of *A. minitissimum* was positively correlated with $\text{NO}_2 + \text{NO}_3$ concentrations in the streams. As a matter of fact, *A. minitissimum* is known to have a high demand for N (Fairchild et al., 1985; Carriok and Lowe, 1988) and is considered to be a pollution-tolerant species in many temperate streams (Krstić et al., 1997; Kwandrans et al., 1997; Soininen and Niemelä, 2002). Correlation with environmental variables also showed that *Nostoc* spp., *D. vulgaris*, *E. minutum*, *N. sinuate* var. *tabellaria*, *R. sinuate*, and *S. ungeriana* var. *pseudogaillonii* were positively correlated with $\text{NO}_2 + \text{NO}_3$ concentrations. *E. minutum* has been observed in areas with high and low nutrient concentrations (Rier and Stevenson, 2006). In this study, however, *E. minutum* was only observed in regions with high $\text{NO}_2 + \text{NO}_3$ concentrations. These species might also be considered to be N-tolerant taxa (Fairchild et al., 1985; Rott et al., 1998; Winter and Duthie, 2000; Winter et al., 2003).

TP was suggested as being an important factor influencing the abundance and composition of diatoms in streams (Soininen and Könönen, 2004). Todd et al. (1996) found that phosphate enrichment increased the proportions of smaller algae. In this study, TP concentrations were not a primary factor structuring the epilithic algal communities in the streams. However, the abundance of *C. placentula* was found to be positively correlated with increased TP concentrations. *C. placentula* is typical of meso- or

eutrophic taxon, and the optimum concentration of TP for growth was $27\text{--}396 \text{ }\mu\text{g L}^{-1}$ (Van Dam et al., 1994; Soininen and Niemelä, 2002; Kovács et al., 2007). Although TP concentrations did not differ significantly among any regions, a clear seasonal pattern did emerge, especially in summer and fall, when the discharge increased. At that time, *C. placentula* replaced *A. atomus* and became the most dominant species in this region. However, the abundance of *C. placentula* quickly decreased in winter when the discharge and TP concentrations in the stream dropped.

Oscillatoria was frequently observed in streams with high nutrient loading and slower current velocities. *Oscillatoria* is also considered to be a pioneer taxon after flooding (DeNicola and McIntire, 1990a; Stevenson, 1996). In the Wuling area, current velocity was slower and $\text{NO}_2 + \text{NO}_3$ concentrations were higher in Yousheng Stream. However, *Oscillatoria* was not the dominant taxon in Yousheng Stream. Instead, *Oscillatoria* was found to be more abundant in the lower reach of Cijiawan Stream, especially in winter. The growth of *Oscillatoria* has been found to be suppressed in high light conditions (DeNicola and McIntire, 1990b). The removal of riparian vegetation from Yousheng Stream might have increased the amount of sunlight reaching the stream surface and thus the water temperature. In the lower reach of Cijiawan Stream, nevertheless, the higher riparian canopy and $\text{NO}_2 + \text{NO}_3$ concentrations were more suitable for the growth of *Oscillatoria*. This suggests that *Oscillatoria* is not a sensitive bioindicator for monitoring agriculture in tropical/subtropical streams.

In addition to the influence of agriculture, the abundance of many diatoms was negatively correlated with grazer density. Grazer density was also identified as one of the major factors affecting spatial changes in epilithic algal community. This suggests a top-down control of epilithic algae by aquatic insects in the stream. Nevertheless, Colletti et al. (1987) indicated that mayflies had little effect on algal assemblages at an insect density of < 1000 individual m^{-2} . In this study, the mean grazer density was only 261–839 individual m^{-2} (Table 1). However, a higher proportion of caddisflies, a grazer, was observed in the streams (Kuo and Chiu, 2005). The mouthparts of caddisflies can scrape attached algae off hard surfaces more effectively than the brush-like mouthparts of most mayfly nymphs (Peterson et al., 1998; Holomuzki and Biggs, 2006). This may be the reason that grazing effects on the abundance of epilithic algae were detected in the streams despite the low density of grazers. Grazing effects on the community composition of epilithic algae need to be further examined.

CONCLUSIONS

The effects of agriculture on the subtropical streams of the Wuling area were significant and varied with the extent of agriculture in the catchment. The epilithic

algal communities were primarily affected by $\text{NO}_2 + \text{NO}_3$ concentrations in the streams resulting from agricultural runoff. The epilithic algal biomass increased with $\text{NO}_2 + \text{NO}_3$ concentration. Correlation analyses further identified the cyanobacteria *Nostoc* spp. and the diatoms *A. minitissimum*, *A. atomus*, *D. vulgaris*, *E. minutum*, *N. sinuata* var. *tabellaria*, *R. sinuate* and *S. ungeriana* var. *pseudogaillonii* as N-tolerant taxa. The diatoms *C. placentula*, *G. tergestinum* var. *tergestinum*, and *Gomphonema* sp.1 were more-closely related to increased TP concentrations. Changes in abundance and community structure of epilithic algae can be used to monitor the effects of agriculture in tropical/subtropical mountain streams.

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農業活動對於亞熱帶台灣高山溪流石附生藻類豐度及群集之影響

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武陵地區溪流是瀕臨滅絕台灣櫻花鉤吻鮭的唯一棲地。本研究目的為瞭解該溪流主要初級生產者—石附生藻類之豐度及群集結構，同時探討沿岸農業活動對於石附生藻類之影響。研究發現本區石附生藻類生物量有明顯之季節變化，在春、冬季較高，夏、秋季較低，且具高度農業活動之有勝溪，藻類生物量明顯較其他溪流為高。本區石附生藻類 85% 是矽藻，其中以 *Achnantheidium* 數量最多。石附生藻類群集亦明顯呈現時空變化。以 BIOENV 分析，發現水溫、導電度、 NO_2+NO_3 與 SiO_2 濃度及流速與石附生藻類群集的季節變化最為相關，而影響藻類群集空間分布差異之主要因子為 NO_2+NO_3 與 SiO_2 濃度以及藻食者密度。本研究顯示石附生藻類之豐度及群集結構變化可用來監測熱帶及亞熱帶地區高山溪流農業活動的影響。

關鍵詞： 武陵；矽藻；*Achnantheidium*； NO_2+NO_3 ；流速；藻食者密度。

