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The effects of phosphorus enrichment on leaf litter stoichiometry in a forested stream

Bryant Baker
University of Arkansas, Fayetteville

The Effects of Phosphorus Enrichment on Leaf Litter Stoichiometry in a Forested Stream

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Bryant Baker

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J. Thad Scott, Ph.D., Chair

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Duane Wolf, Ph.D.

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Michelle Evans-White, Ph.D.

I. Summary

The effects of nutrient (N and P) enrichment on leaf litter decomposition in streams have been investigated extensively, but few have explored how P addition alone affects leaf litter stoichiometry (namely the C:P ratio). This study examined how the P content, C:P ratio and decomposition of two types of leaf litter (the recalcitrant *Quercus stellata* and the more labile *Acer saccharum*) responded to P enrichment from nutrient diffusing substrata (NDS) which was either unenriched agar or agar enriched with a moderate or high level of P. Leaf litter was sealed in 0.05 mm mesh bags, which excluded invertebrates, housed with NDS inside unique PVC containers and placed in an Ozark stream. Leaf C, P, and dry mass remaining were measured for 154 days. A linear regression analysis was run on the response ratio (RR; ratio of treatment value to control value for a sampling date) for leaf litter P and leaf litter C:P of each leaf type to test the null hypothesis that the slope was equal to 0. There was no effect of P enrichment on the decomposition of either oak or maple leaf litter. The moderate P treatment had no effect on leaf litter P or C:P, therefore the response ratios were calculated using only the high P and control values. The RR of leaf litter P (m = 0.0023, $P = 0.0293$) and leaf litter C:P (m = -.0016, $P = 0.0294$) of oak both indicated a significant increase in leaf litter P and decrease in leaf litter C:P with P addition through time. The same was true for the RR of maple leaf litter P (m = 0.0041, $P = 0.0076$) and leaf litter C:P (m = -0.0030, $P = 0.0120$). My results indicated that P enrichment did increase P content and decrease the C:P ratio of both oak and maple leaf litter. Maple leaves responded to enrichment faster and at a greater magnitude than oak leaves, possibly due to their greater carbon lability.

II. Introduction

For the last century, humans have greatly impacted the global biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P). Human activity, namely agriculture, has affected the inputs and outputs of these elements on terrestrial and aquatic systems. For example, the rate of N input into the terrestrial N cycle has approximately doubled with anthropogenic N inputs currently adding at least as much fixed N to terrestrial ecosystems as do all natural sources combined (Smith et al., 1999). Human activity has also heavily impacted the fluxes of P to terrestrial ecosystems. Large quantities of P are added as fertilizers and animal manures and in many areas P inputs from these sources exceed P outputs in farm produce (Carpenter et al., 1998). While the addition of these nutrients has had positive effects such as increased crop yields in some areas, there have also been negative impacts on not only terrestrial ecosystems, but aquatic ecosystems as well. One such negative impact on aquatic ecosystems is eutrophication, or an increase in primary productivity caused by increased concentrations of nutrients, namely N and P.

Freshwater Eutrophication

Enrichment of freshwater with N and P can accelerate the process of eutrophication and is arguably the most common impairment of surface waters in the United States (Carpenter et al., 1998). The majority of research on freshwater eutrophication has dealt only with the impacts of nutrient enrichment on autotrophic production in lakes and reservoirs (Smith et al., 1999; Dodds, 2007). However, an interest in the effects of nutrient enrichment on streams has developed in recent years.

Stream Eutrophication: Effects on Submerged Leaf Litter

A main focus of stream eutrophication research has dealt with the effects of dissolved N and P on the decomposition of submerged, allochthonous detritus (dead organic matter) such as leaves. Allochthonous leaf litter drives stream metabolism and productivity in forested headwater streams (Wallace et al., 1997). The rate of leaf litter decomposition is determined by various factors. The lignin content in a leaf has been determined to be one of these factors with leaves containing high amounts of lignin having slower decomposition rates (Gessner and Chauvet, 1994). Melillo et al. (1982) concluded that the mass of leaves remaining after decomposing for twelve months was positively correlated with the ratio of initial leaf lignin to initial leaf N. The percentage of total leaf C as lignin and the lignin concentration are good indicators of relative decomposition rates for various tree species (Royer and Minshall, 2001).

Another factor that can control detritus decomposition is the nutritional quality of the substrate. Microbial respiration rates on leaves are typically higher than on woody particulates (Stelzer et al., 2003) suggesting that decomposition may be slower in substrates with a higher C:N ratio. This may occur because microbes colonizing substrates with high C:N ratios are more nitrogen limited, thus slowing growth rates and subsequently substrate decomposition rates. However, the C:N ratio does not always correspond to the order of breakdown among different species (Royer and Minshall, 2001).

Interest in stream nutrient levels has grown due to the idea that heterotrophic fungi and bacteria decomposing submerged leaves (from which they get their carbon) can obtain N and P from the water column (Howarth and Fisher, 1976), especially when detritus nutrient levels are low (e.g. Caraco et al., 1998). Therefore nutrient enrichment of streams can increase leaf litter microbial biomass and decomposition (Howarth and Fisher, 1976; Elwood et al., 1981; Stelzer et

al., 2003; Gulis et al., 2006; Greenwood et al., 2007) and subsequently secondary production by invertebrates associated with leaf litter (Cross et al., 2006). However, enrichment of streams that have relatively high background concentrations of N and P has little to no effect on leaf litter decomposition because neither N nor P are limiting to microbial growth (Royer and Minshall, 2001; Abelho and Graça, 2006).

Aquatic fungi typically contribute more to leaf decomposition than do bacteria and have higher amounts of biomass (e.g. Gessner and Chauvet, 1994; Gulis and Suberkropp, 2003a; Gulis and Suberkropp, 2003b; Baldy et al., 2007). Additionally, fungal biomass and respiration rates are typically lower in hypereutrophic streams compared to eutrophic streams, but still proportionally higher than bacterial biomass (Baldy et al., 2007; Duarte et al., 2009) possibly indicating fungal sensitivity to higher levels of inorganic nutrients. The relative proportions of fungal and bacterial biomass are perhaps more important in terms of leaf litter stoichiometry. Decreases in leaf litter C:P with elevated N and P levels coincided with an increase in fungal and bacterial biomass on leaves in a long-term nutrient enrichment experiment at the Coweeta Hydrologic Laboratory, suggesting that microbes can substantially contribute to changes in leaf P content in response to nutrient enrichment (Cross et al., 2003; Suberkropp et al., 2010). Changes in food resource elemental ratios can decrease invertebrate diversity and species richness in streams (Evans-White et al., 2009). These bottom-up effects on the food web in response to nutrient enrichment may have widespread implications for food web production as well as resilience.

Despite the increased amount of research on the effects of nutrient enrichment on leaf litter dynamics in streams in recent years, the literature is still lacking various key data. As pointed out in Stelzer et al. (2003), the effects of P enrichment alone on leaf litter decomposition

and stoichiometry in streams have not been extensively researched (however, see Abelho and Graça, 2006). Thus, the effect of P enrichment on various microbial processes such as C mineralization (respiration) and microbial P assimilation and immobilization in P limited streams is still unclear. Also, the one study that has experimentally examined leaf litter C:P through time in response to nutrient enrichment, did not attempt to exclude invertebrate detritivores, did not treat with P only, and sampled mixed leaf litter, which did not take substrate lability into account (Cross et al., 2003). Therefore the overall objective of this study was to determine what effects P enrichment had on the decomposition and leaf litter C:P ratio of two leaf types of different levels of lability in a forested stream.

III. Research Hypotheses

There were three main hypotheses for this study:

Hypothesis 1. The rate of mass loss (decomposition) will be higher in the more labile leaf type (maple) compared to the less labile leaf type (oak) and will be positively affected by P addition.

Hypothesis 2. The P content (%P) of both leaf types will increase through time and increase with increasing P addition.

Hypothesis 3. The rate of C:P (molar) decline (i.e. an increase in the P content and a decrease in the C content) of both leaf types through time will be higher when P is added than with no P addition.

IV. Materials and Methods

Study Site

My study was conducted in Jones Creek, a third-order stream near Winfrey Arkansas. Jones Creek has relatively low concentrations of SRP (< 2 μg/L) and moderate nitrate + nitrite (345 ± 32 μg/L). The land use of the 51 km^2 drainage area of Jones Creek is characterized by mostly forest with interspersed pasture. The stream reach used in this study was located upstream of the confluence of Jones Creek and Frog Bayou, a stream that flows into the surrounding area's drinking water reservoir, Lake Fort Smith. Jones Creek has a USGS gauging station slightly downstream of the study site which continuously monitors discharge. During the study period, discharge was low during days 1 through 76 (0.18 $m^3 s^{-1}$ on average) of the experiment and relatively higher between days 77 and 154 (1.03 $m^3 s^{-1}$) reaching up to 11.0 $m^3 s^{-1}$ on day 150 (Fig. 1). Throughout the study period the average discharge was 0.60 $m^3 s^{-1}$.

Leaf Litter and Mesh Bags

Two leaf species were used in this study: sugar maple (*Acer saccharum* Marsh.) and post oak (*Quercus stellata* Wangenh.); these leaf species will be referred to as simply maple and oak hereafter). Leaves were collected shortly after abscission and air-dried to a constant weight. To increase pliability before cutting, leaves were presoaked in DI water. Approximately 2 cm^2 leaf sections were cut and placed into 0.05 mm mesh bags (Ankom® Concentrate Bags). The bags were dried at 50 °C for 48 hours, sealed, and weighed to the nearest mg. Each bag contained 1.0 – 1.5 g of either maple or oak leaf material (dry weight).

The leaf litter bag mesh size was chosen so that invertebrate shredders would be excluded. Most leaf litter decomposition studies attempting to exclude invertebrates use 0.3 - 1

mm mesh sizes; however, this may not be excluding shredders from the Chironomidae family which can pass through mesh sizes as small as 0.125 mm (Storey and Pinder, 1985; Hudson and Adams, 1998). This can be especially important in temperate streams where chironomids may account for up to 60% of invertebrates colonizing leaf litter (Gonçalves et al., 2007). Chironomid biomass on leaf litter has also been shown to increase with P enrichment (Rosemond et al., 2001), lending further credence to the use of a mesh size that will exclude all chironomids in this particular study.

Nutrient Diffusing Substrata

Nutrient diffusing substrata (NDS) were used to enrich the leaf litter with P. In this study, 2% agar was used as the NDS medium, housed in PVC units of a novel design. The housing unit was designed to force P diffusing from the enclosed agar into the main portion of PVC housing the leaf litter bags (Fig. 2). All housing units contained agar with one of three treatments: no P (control), 0.201 g P L agar^{-1} (moderate P), or 2.01 g P L agar^{-1} (high P).

A preliminary experiment was conducted in order to determine P diffusion rates for each treatment. The P-containing agar was made by combining $Na_2HPO_4 \cdot 7H_2O$ with 2% purified agar for a final concentration of 0.201 g P L^{-1} and 2.01 g P L^{-1} for the moderate P and high P treatments, respectively. The control agar was also made with 2% purified agar. Agar from each treatment was autoclaved for 15 minutes at 121 °C, poured into the PVC agar housing units, and allowed to cool overnight. Five agar units for each treatment were then placed into separate 1 L amber bottles with 850 mL of deionized (DI) water on day 0. Water was collected from each bottle on days 1, 2, 4, 9, 13, and 17 and analyzed for SRP by colorimetry using the ascorbic acid

method (APHA, 2007). This preliminary experiment indicated that the agar would need to be replaced every 1-2 weeks in the field in order to sustain P diffusion.

Sampling

A total of 36 NDS units, 12 for each treatment, were placed in Jones Creek on November 16, 2010. The NDS units were placed along four transects at riffles along the stream reach. Water samples were taken between transects to determine if the control units were receiving P from units placed upstream. However, the SRP concentrations measured from these samples were below detection.

One unit from each treatment was retrieved from the stream on days 3, 8, 13, 21, 29, 36, 48, 59, 72, 102, 136, and 154 and taken back to the lab for processing. In the lab, the leaf litter bags were removed and gently rinsed with DI water to remove any debris caught on the bag surface. The bags were then dried for 48-72 hours at 50 °C and weighed to the nearest mg to determine mass loss. The leaves from each treatment were separately ground into a fine powder using a Thomas Wiley® Mini-Mill.

The ground leaf material was stored in the freezer until analyzed for C and N using a Thermo Flash 2000 combustion elemental analyzer and for P using the ascorbic acid method following a modified persulfate digestion (APHA, 2007). For the persulfate digestion, 4-5 mg of dried leaf material was ashed for 4 hours at 500 °C and then added to 15 mL of Nanopure® water and 1.8 mL of 2% peroxydisulfate solution. The leaf material and persulfate solution were then autoclaved for 1 hour at 121 °C, allowed to cool overnight, and analyzed colorimetrically for P using the ascorbic acid method (APHA, 2007). Response ratios in each leaf type were

calculated from %P and C:P measurements. This ratio can illustrate the difference between the treatments when it deviates from being equal to one.

Statistical Measurements

Replication was not possible due to limitations of space and resources. The data are presented in time series plots to show the relative patterns in leaf litter %P and C:P in the various treatments through time. Additionally, I calculated a response ratio (RR) for each leaf species on each date in order to test my hypotheses quantitatively. Briefly, RR was the ratio of the response measured in the high P treatment to the response measured in the control on a given date. The RR was calculated for %P and for C:P for both leaf species. I used linear regression analysis in Sigma Plot 11 to test the null hypothesis that the slope of the RR versus time would be equal to zero. Slopes that were statistically different from zero indicated that the treatment had an effect on the measured response relative to the control.

V. Results

Preliminary Experiment

The moderate P and high P agar diffused on average, 0.681 (± 0.05) and 6.58 (±0.29) mg P respectively, in the first 24 hours after the agar units were placed inside the amber bottles. The rate of P diffusion for the moderate P treatment was described by the equation: $y = 0.685x^{-0.62}$ (Fig. 3). The rate of P diffusion for the high P treatment was described by the equation: $y = 6.299x^{-0.58}$ (Fig. 3), meaning the high P agar would have been diffusing the same amount of P on day 46 as the moderate P agar was diffusing on day 1. Soluble reactive phosphorus was undetectable on all days in the control.

Mass Loss

In both the maple and oak leaf litter bags, there was no significant difference in mass loss of leaf litter among the various P treatments. Therefore, for each leaf species, the three treatments were treated as replicates and averaged together in order to compare differences in decomposition among species. The maple leaf litter showed higher rates of mass loss through time compared to oak leaf litter. Both species exhibited a rapid decrease in percent mass remaining between days 0 and 3. The percent mass of maple leaf litter bag remaining dropped from 100% on day 0 for both species to 93% and 84% on day 3 for oak and maple, respectively. Both species follow a linear rate of mass loss after day 3, with the maple having a higher rate of mass loss. Between days 3 and 154 (excluding the initial percent mass remaining at day 0), the slope of the linear regression for the percent mass of maple leaf litter remaining was -0.138 which was more than twice that of oak which had a slope of -0.057. On day 154, the percent mass remaining for oak and maple was 83.9 and 59.9, respectively (Fig. 4).

Leaf Litter Stoichiometry

There was no observable difference between the control and moderate P treatment for any measurement. Therefore the results presented hereafter only include data from the control and high P treatment.

Both maple and oak leaves experienced similar patterns in %P change through time. Each leaf type had high initial %P with values of 0.096 and 0.080 for maple and oak, respectively. However, by day 3 %P of each leaf type in both treatments had decreased substantially. Oak and maple %P values dropped to below 0.050 and 0.040, respectively (Fig.

5). Each leaf type experienced high %P variability in both the control and high P treatment for the beginning of the experiment. However, the maple leaf litter began to show a distinction between the treatments on day 48 whereas the oak leaf litter treatments retained similarity until day 102 (Fig. 5). The high P maple leaf litter %P increased to a maximum of 0.083 on day 136 and 0.060 on day 154. Similarly, the % P in the high P oak leaf litter increased to 0.075 and 0.065 on days 136 and 154, respectively. Both types of leaf litter in the control on days 136 and 154 had %P values ranging between 0.047 and 0.054 (Fig. 5).

The leaf litter %C was also measured in order to obtain C:P values. There was a relatively small decrease in oak %C throughout the study. Oak %C values in the high P treatment ranged from 48 on day 8 to 45 on day 154 (Fig. 6A). This range was similar to the control (48 on day 8 and 45 on day 102). Maple %C values decreased slightly more than oak %C values, ranging from 46 on day 3 to 40 on day 154 in the control and from 46 on day 8 to 41 on day 154 in the high P treatment (Fig. 6B).

Oak leaf litter C:P in both the control and high P treatment ranged from approximately 2200 to 3100 for the first 72 days of the experiment (Fig. 7A). After day 102, the treatments appear to separate with C:P values in the high P treatment dropping below 2000 (as low as 1587 on day 136) on each subsequent sampling date while control values remained above 2200 (Fig. 7A). Maple C:P values for both treatments ranged from approximately 2150 to 3600 for the first 36 days of the experiment. Beginning on day 48, C:P values began to differentiate between the control and high P treatment. The C:P values in the high P treatment fell below 2000 (as low as 1340 on day 136) on each of the last three sampling dates while the C:P in the control remained above 2200 (Fig. 7B).

The oak RR for %P ranged from 1.09 to 0.91 for the first 102 days of the experiment. The slope of a linear regression was significantly different from 0 (m = 0.0023, r^2 = 0.392, P < 0.05), indicating a significant difference between the high P treatment and control. On days 136 and 154, this ratio reached values of 1.58 and 1.19, respectively (Fig. 8A), indicating larger differences between treatments compared to the beginning of the experiment. The slope of a linear regression for the maple %P RR was significantly different from 0 (m = 0.0041, r^2 = 0.526, P < 0.01). The RR values ranged from 1.16 to 0.80 during this period. By day 59 the RR consistently remained above 1.19 with values reaching 1.44, 1.56, and 1.66 on days 59, 102, and 136, respectively (Fig. 8B). Although the regression was leveraged by the value measured on day 136, no data was excluded from the analysis and the slope was statistically significant.

The RR linear regression for oak C:P indicated that the high P treatment was significantly different from the control (m = -0.0016, r^2 = 6.443, P < 0.05). The RR for oak C:P remained between 1.09 and 0.90 for the first 102 days of the experiment. A larger deviation from 1.0 occurred on days 136 and 154 with values of 0.62 and 0.81, respectively (Fig. 9A). The linear regression for the RR of maple C:P also showed a statistically significant difference between the high P treatment and control (m = -0.0030, r^2 = 0.484, P < 0.05). The RR for maple C:P was, like the %P RR values, variable for the first 49 days of the experiment. These values ranged from 1.22 to 0.86 during this period. The RR then consistently fell below 0.85, even to as low as 0.58 on day 136 (Fig. 9B).

VI. Discussion

Mass Loss

The mass loss rates recorded for both oak and maple leaves in my study are lower than what has been reported for both oak and maple leaves in other literature (Gessner and Chauvet, 1994; Gulis et al., 2006; Greenwood et al., 2007). However, the mesh size of the leaf litter bags used in my study was 1-2 orders of magnitude smaller than has typically been used to exclude invertebrates and probably more successful in excluding all shredders. The presence of shredders tends to increase leaf litter decomposition rates (Bergfur et al., 2007; Gonçalves et al., 2007). However, the mass loss results of my study did fall into the range found by Bergfur et al. (2007) in which 0.3 mm mesh litter bags were used to measure alder leaf decomposition. This mesh size may have been more efficient than the 0.5 – 1.0 mm mesh bags in excluding chironomids.

In both leaf types, the data from each treatment being so similar may have been due to the lack of invertebrates, particularly shredders. Oak and alder leaves in two Portuguese streams showed much less of a response to eutrophication when enclosed in 0.5 mm mesh bags compared to 10 mm (Gulis et al., 2006). Shredders play an important role in fragmenting the leaf material, but may not contribute as much to leaf litter P due to their inability to immobilize inorganic P from the water column and their relatively low biomass compared to microbial decomposers (Baldy et al., 2007).

The maple leaf litter exhibited a more rapid mass loss than oak leaf litter as was expected. This was most likely due to the higher recalcitrance of oak leaf material as mainly defined by higher lignin content (Melillo et al., 1982; Gessner and Chauvet, 1994). The rapid mass loss of both leaf types between days 0 and 3 may be due to nutrient release caused by leaching. Shieh et

al. (2008) found that most leaf nutrients experienced leaching in the first 1-3 days. Other leaf litter decomposition studies have also reported rapid mass loss (20-40%) in the first week of experimentation despite differences in litterbag mesh size or leaf type (Gessner and Chauvet, 1994; Royer and Minshall, 2001; Baldy et al., 2007).

Leaf Litter Stoichiometry

Initial %P values of both leaf types were higher than have been reported in other studies examining *A.saccharum* and various *Quercus* species (Gessner and Chauvet, 1994; Stelzer et al., 2003) which may be due to the different ecosystems where the leaves were collected (e.g. areas where soil nutrient concentrations are higher). Both leaf types showed a rapid decrease of %P in each treatment between day 0 and day 3, which is consistent with the findings of other studies (Abelho and Graça, 2006; Menéndez et al., 2011). This was most likely due to rapid P leaching with the amount lost in the first three days comparable to results found by Shieh et al. (2008).

Oak %P was less variable, steadily decreasing until day 29 after which %P increased until day 154, between sampling days in the high P treatment compared to maple (Fig. 5A). This increased variability in the more labile leaf type has been found in other studies as well (Gulis et al., 2006). The higher %P variability during the first 36 days in the maple leaf litter may have been related to a period of microbial colonization, particularly by microfungi. Variability in fungal biomass and species richness in response to nutrient enrichment on more labile substrates such as maple leaves is often higher compared to more recalcitrant material (Gulis and Suberkropp, 2003; Gulis et al., 2006; Harrop et al., 2009). This may be due to stable communities finding niches in the breakdown of the less labile oak leaves, resulting in steady P immobilization (or release in the beginning). The increased leaching in the less recalcitrant leaf

type (Shieh et al., 2008) may be increasing competition for early colonizers due to the wider availability of nutrients such as P. As well, the P diffusing from the agar was actually being supplied to microbial communities in pulse events (high diffusion in the first three days; Fig. 3), which may have increased competition and caused variable colonization. By day 48, when the maple leaf litter begins to show a steadier increase in P (as well as differentiation between treatments), the microbial community may have become more established and stable, thus allowing for turnover of microbial biomass P, as well as P immobilization from the agar diffusion.

It is interesting to note that, while %P in both leaf types eventually increased in the high P treatment, neither leaf %P returned to 100% of initial P content as of day 154 resulting in the leaf litter being a net P source rather than a net sink. This is not what has been observed in other studies, where %P did initially decrease, but returned to or exceeded initial levels (Cross et al., 2003; Abelho and Graça, 2006; Menéndez et al., 2011). However, these studies either did not attempt to exclude invertebrates or used litterbags with a mesh size (0.5 mm) that may have allowed for colonization by chironomids.

The initial C content of both leaf types was consistent with what has been reported in other studies (Elwood et al., 1981; Ostrofsky, 1997; Stelzer et al., 2003). The leaf %C did not appear to be affected by P enrichment for either leaf type. However, maple did show a noticeably larger decrease in %C throughout the experiment (Fig. 6B). This is not consistent with other studies testing decomposition in response to enrichment (Menéndez et al., 2011), but Shieh et al. (2008) did find that %C decreased considerably in some species due to leaching.

Oak and maple C:P eventually decreased to lower levels in the high P treatment compared to the control. The lower C:P levels reached by maple may have been due, in part, to

the larger decrease in %C compared to oak leaves, as %P in both leaf types was similar. This leaf litter C:P decrease in response to P enrichment is consistent with results from a whole stream enrichment of mixed leaf litter packs, including invertebrates (Cross et al., 2003). The RR for %P and C:P in both leaf types eventually deviated from one, indicating that P enrichment did have an effect on %P and subsequently C:P. If the leaf bags had been continuously enriched with the same level of P, rather than in pulse events, the RR would possibly have deviated from one much sooner. However, P enrichment was not necessarily consistent due to the diffusion rates exponentially decreasing after being replaced with fresh agar. This disparity in P enrichment was probably the cause of much of the variability in this experiment and should be addressed in future studies.

The results from my study demonstrated that P enrichment can affect the stoichiometry of oak and maple leaf litter, but not the decomposition rates. Results also indicated that more labile leaves show a greater response to P enrichment, but increased variability. The increases in leaf %P and subsequent decreases in leaf litter C:P can have many implications for bottom-up effects in detrital-based lotic ecosystems. Stoichiometric imbalances between consumers and food resources have been well-documented (Sterner and Elser, 2002), but research is lacking on exactly how the nutrient content of detrital resources in streams is affected by nutrient enrichment. This study is important in terms of how food resource stoichiometry can be influenced by microbial decomposers (when shredders are absent) in response to P enrichment. An increase in food resource P content, as was found in my study, can cause invertebrate consumers to deviate from strict homeostasis by increasing P storage (Cross et al., 2003) as well as increase invertebrate growth rates (Frost and Elser, 2002). Likewise, an increase in C content of food resources such as algae (with high production from an increase in light availability) can

inhibit the production of P-rich grazers due to a substantial increase in food resource C:P (Sterner et al., 1998). Thus it is important to better understand these stoichiometric imbalances in order to predict food web changes in response to disturbance. Such predictions could be useful in determining how certain lotic ecosystems deal with the increasing problem of eutrophication.

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Figures

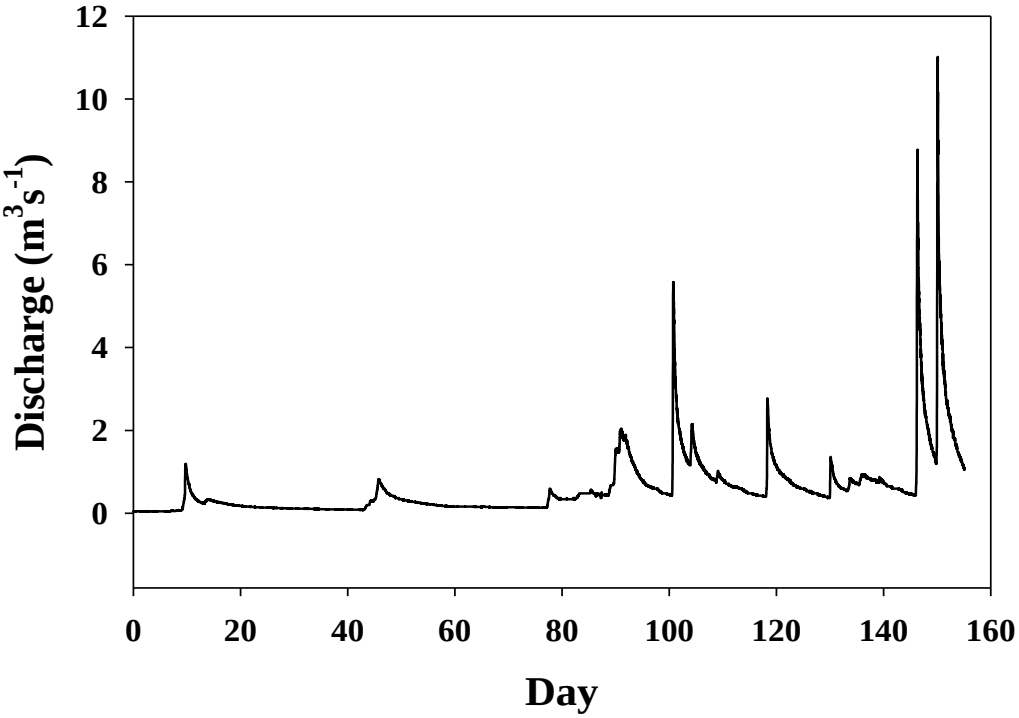


Fig. 1. Jones Creek discharge during study period. Data collected from USGS gauging station 07250935 near Winfrey, AR.

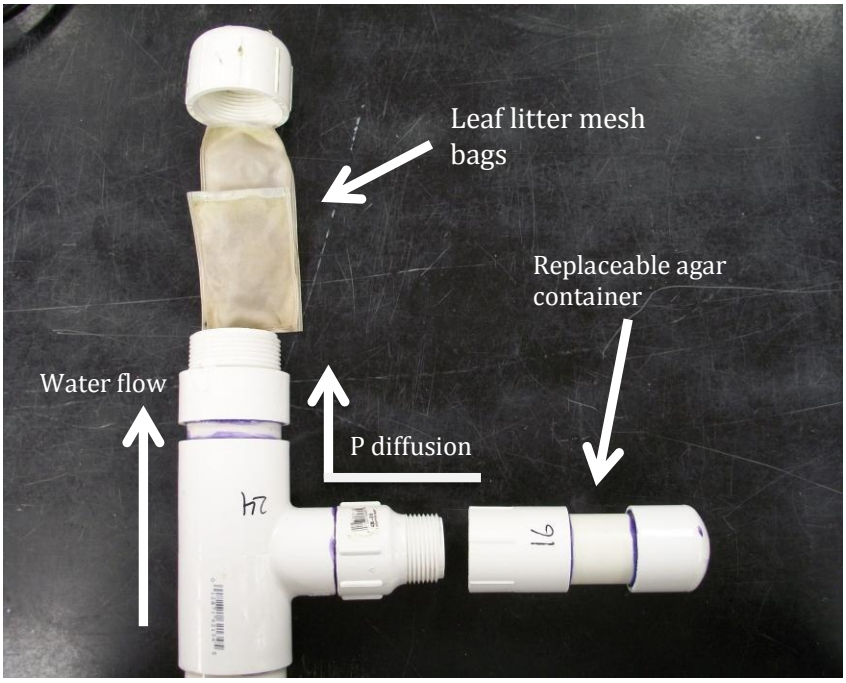
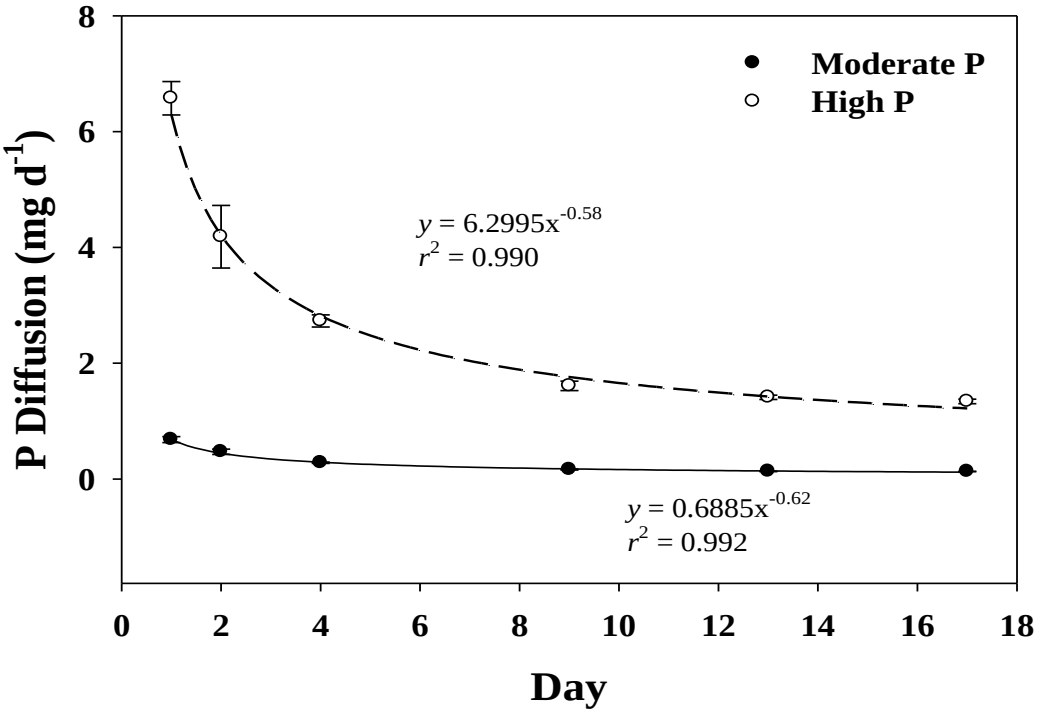


Fig. 2. NDS apparatus design.



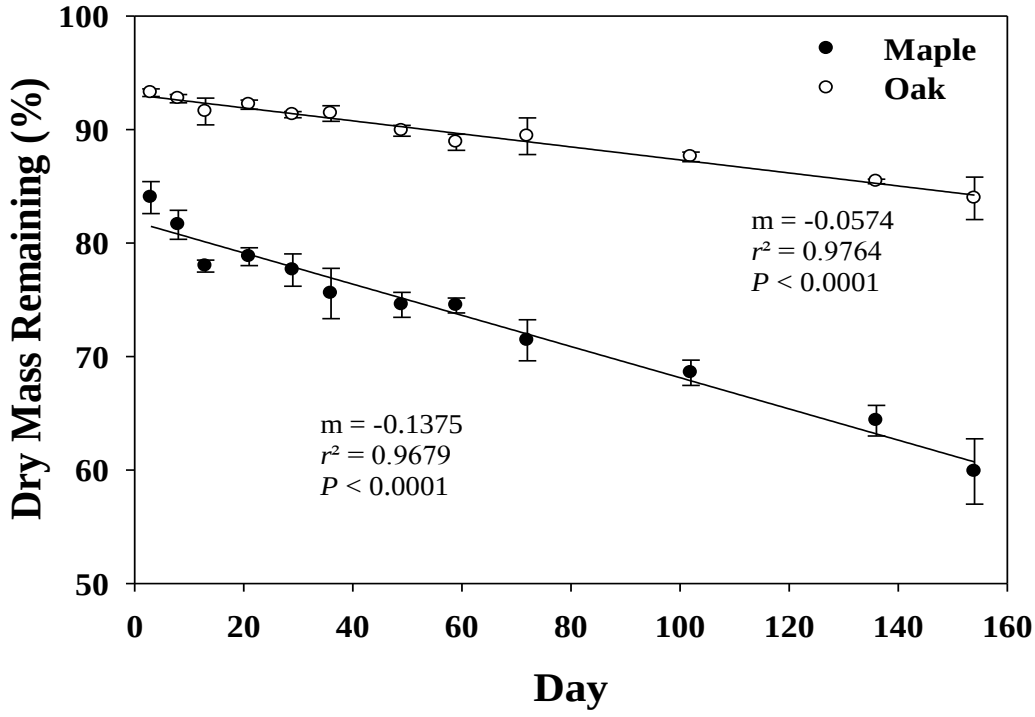


Fig. 3 (top) P diffusion from moderate P and high P agar during preliminary experiment. **Fig. 4** (bottom) Leaf litter dry mass remaining, as a percentage of the initial litterbag weight, throughout experiment. Linear regressions were run on data from day 3 through end of experiment.

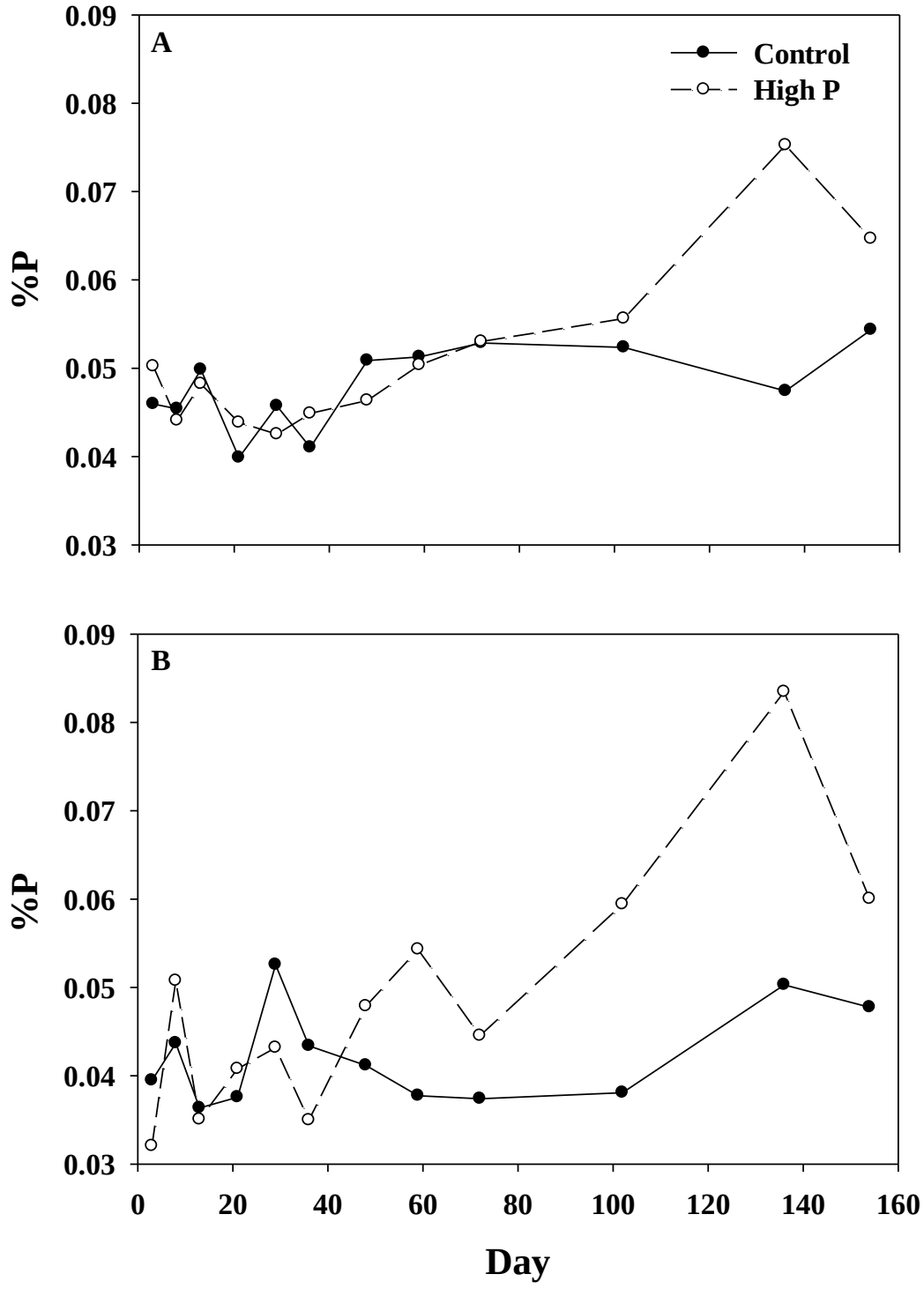


Fig. 5. Oak %P (A) and maple %P (B) shown through time. %P is by weight.

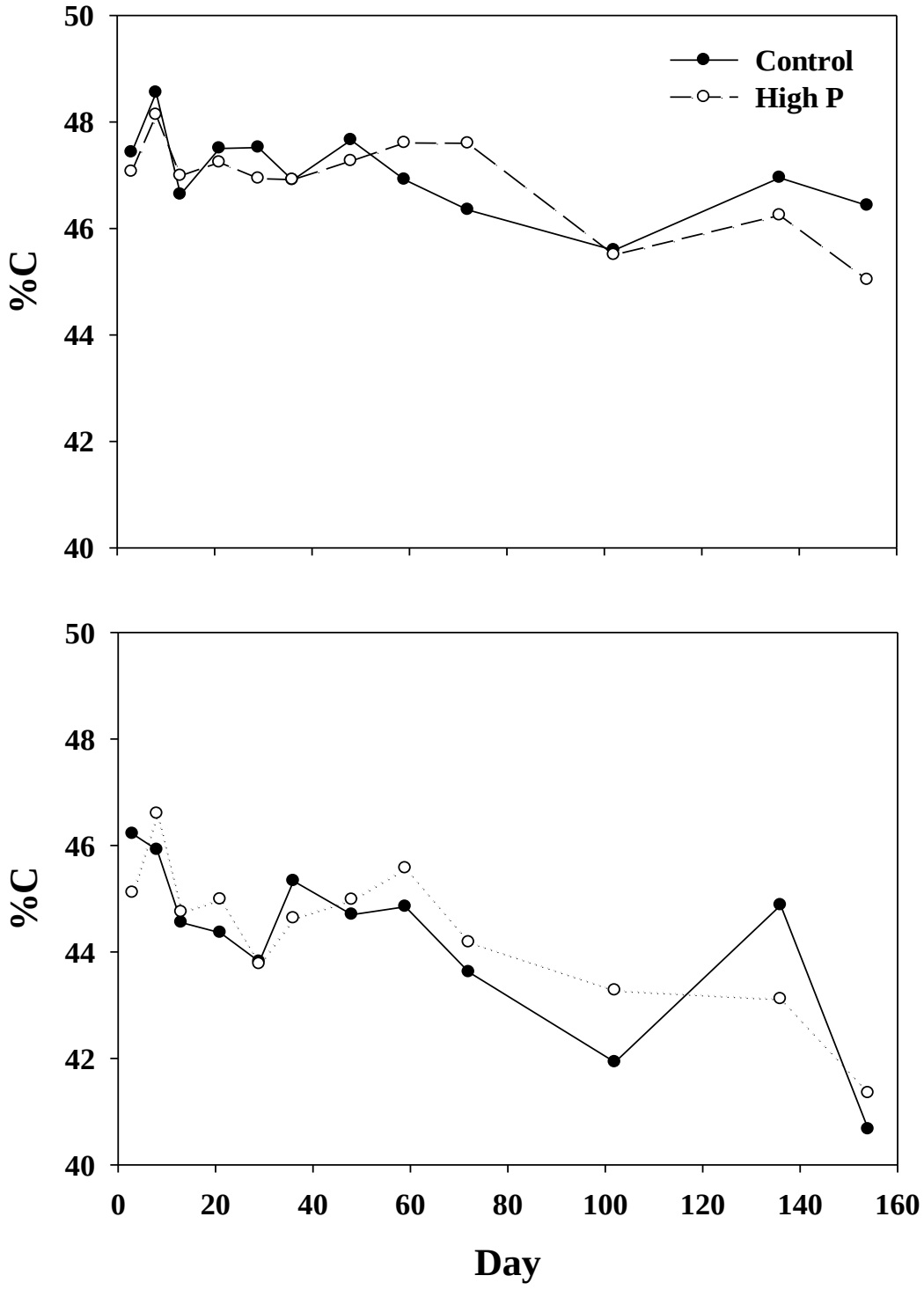


Fig. 6. Oak %C (A) and maple %C (B) shown through time. %C is by weight.

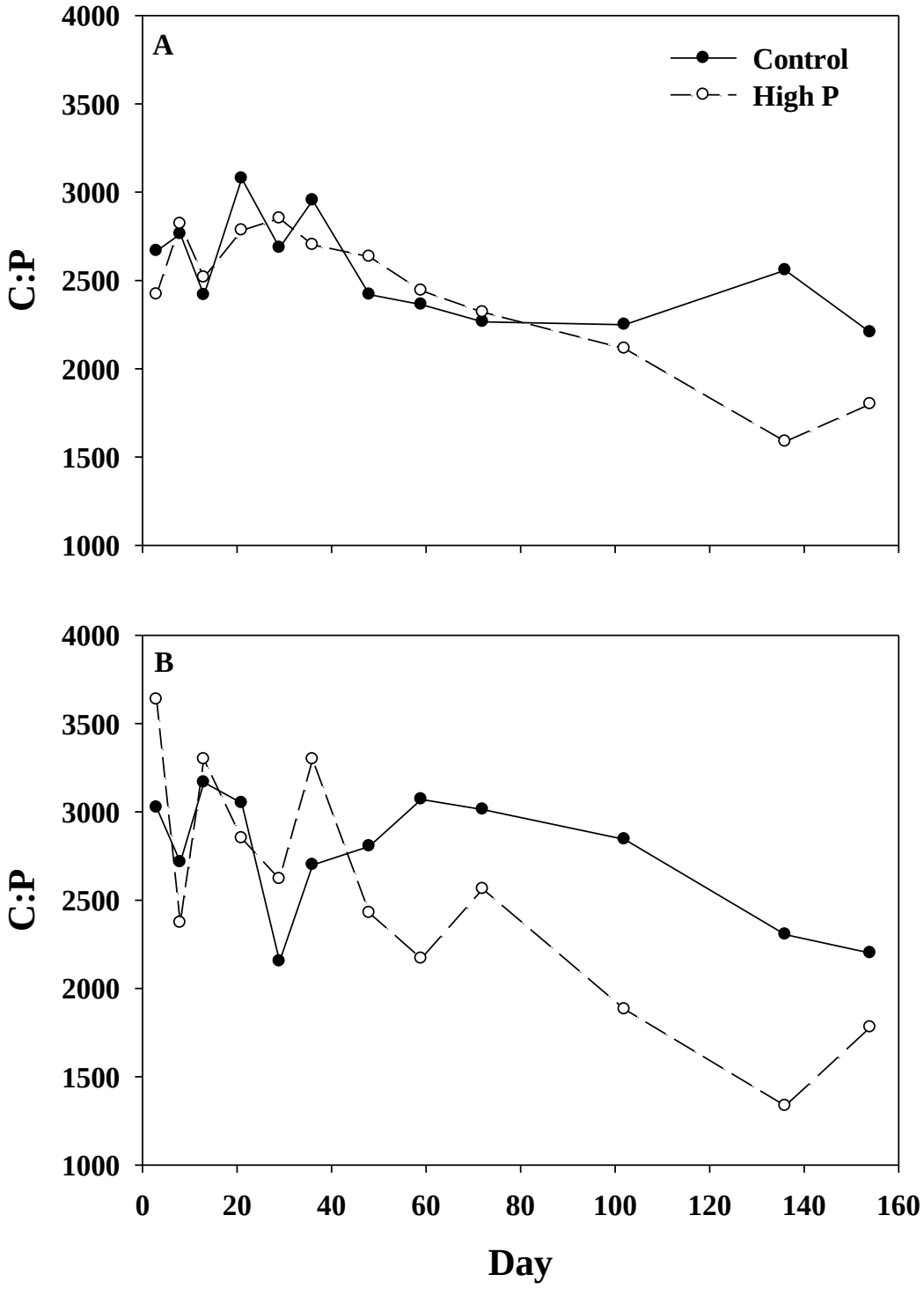


Fig. 7. Oak C:P (A) and maple C:P (B) shown through time. C:P is on a molar basis.

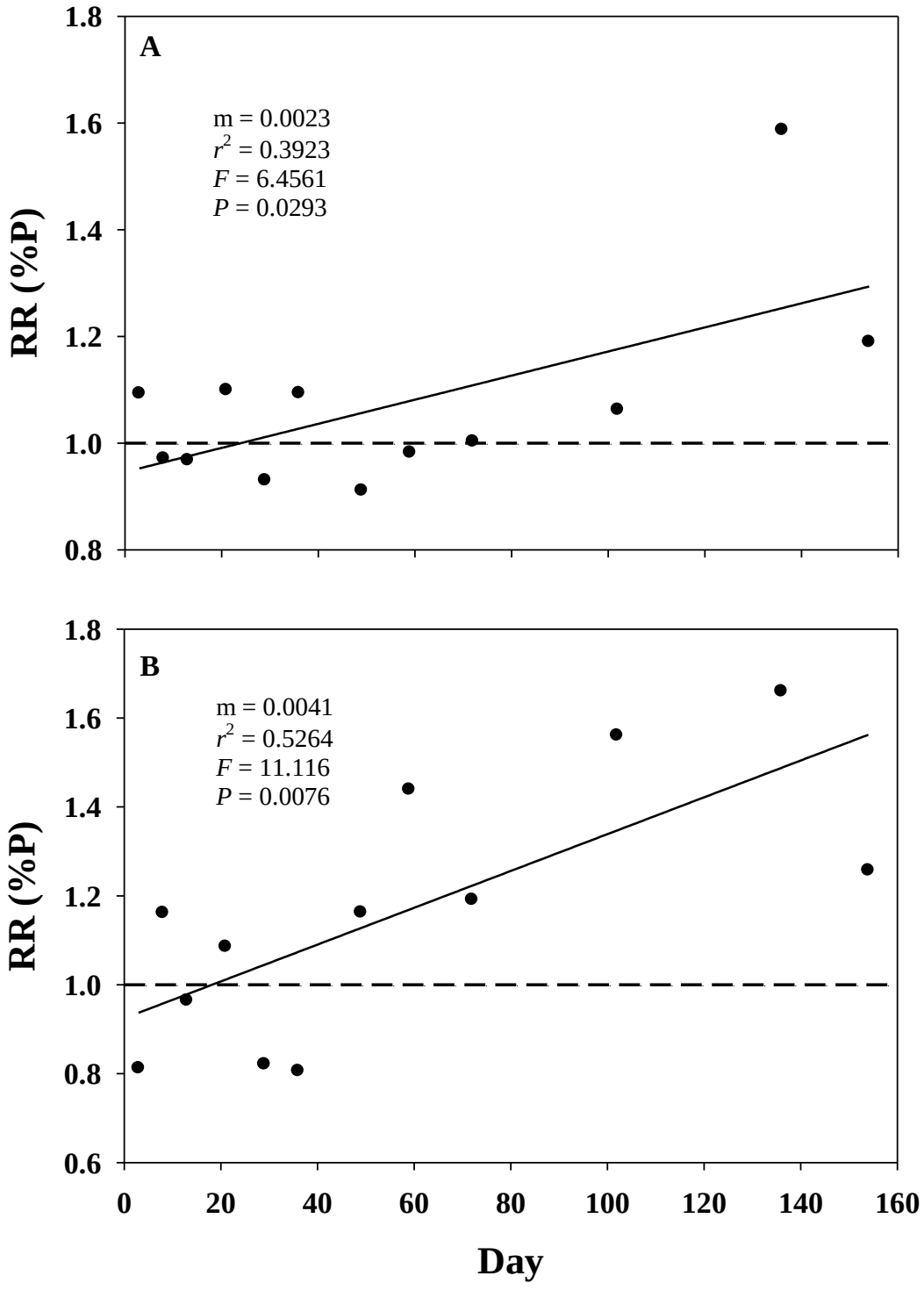


Fig. 8. %P RR shown for oak (A) and maple (B) leaf litter throughout experiment. Reference line at 1 to show no difference between treatments.

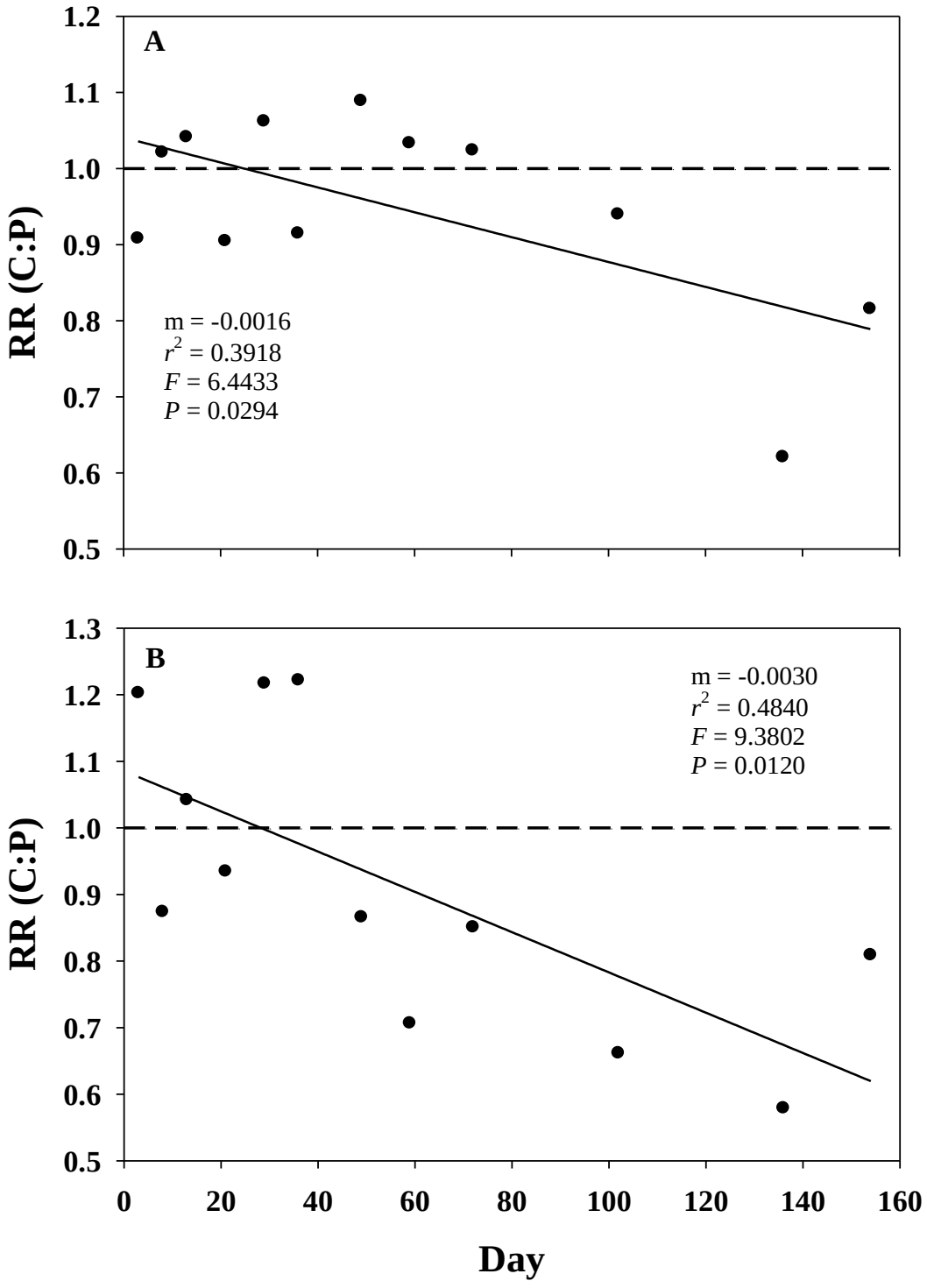


Fig. 9. C:P RR shown for oak (A) and maple (B) leaf litter throughout experiment. Reference line at 1 to show no difference between treatments.