

Species Traits, Species Richness and the Resilience of Wetlands after Disturbance

KATHARINA A. M. ENGELHARDT^{1,2} AND JOHN A. KADLEC¹

ABSTRACT

Recent studies on grasslands demonstrate that species losses and subsequent changes in diversity can decrease the resilience (recovery ability) of ecosystems after a disturbance and can alter ecosystem functioning (e.g., productivity). These studies also explain that responses of ecosystems to en-

vironmental perturbation or species loss ultimately depend on individual species traits and species interactions within a community. We conducted an experiment with 220 wetland mesocosms in summer 1998 to test whether species richness or presence of specific species of submersed aquatic plants (*Potamogeton pectinatus* L., *Potamogeton nodosus* Poir., *Potamogeton crispus* L., *Zannichellia palustris* L., and *Ruppia maritima* L.) affect the resilience of macrophyte above-ground biomass and total ecosystem respiration after disturbance (clipping). Neither respiration or final biomass were affected significantly by macrophyte species richness. Species richness also did not have a significant effect on the resilience of macrophyte biomass and system respiration. In contrast, the presence of specific species had significant effects on macrophyte biom-

¹Utah State University; Department of Fisheries and Wildlife and The Ecology Center, 5210 Old Main Hill, Logan, UT 84321-5210.

²Current address: University of Maryland, Center for Environmental Science, Appalachian Laboratory, 301 Braddock Road, Frostburg, MD 21532-2307. E-mail: engelhardt@al.umces.edu. Received for publication July 25, 2000 and in revised form September 10, 2001.

ass, respiration and the resilience of these processes. This study demonstrates that species roles and impacts need to be considered when assessing the effects of biodiversity loss on ecosystem functioning and resilience. This information is vital in the effective management, conservation, restoration, and creation of functioning wetlands.

Key words: biodiversity, biomass, respiration, clipping, *Potamogeton pectinatus* L., *Potamogeton nodosus* Poir., *Potamogeton crispus* L., *Zannichellia palustris* L., *Ruppia maritima* L.

INTRODUCTION

Studies on the effects of species diversity on the sustainability and functioning of ecosystems are becoming increasingly important in ecological research, owing to increasing species extinction rates and alteration of ecosystems to better serve human needs. One question commonly asked in this research is "how could species loss and changes in community composition affect ecosystem functioning, resilience after a disturbance, and services to humans?" Such research generally concludes that high biodiversity enhances ecosystem stability and functioning because high biodiversity increases the probability that some species within the community are adapted to changes in environmental conditions, thus buffering ecosystem processes against short-term disturbance and long-term environmental change (the "diversity-stability" hypothesis; McNaughton 1977, Pimm 1984, Berish and Ewel 1988, Vitousek and Hooper 1993). Furthermore, high biodiversity increases the probability that all niches within the environment are filled, thus increasing utilization of the environment (the "diversity-productivity" hypothesis; Naeem et al. 1994, 1995, 1996, Tilman et al. 1996). In contrast, ecosystem processes may not be related to diversity when different species play similar roles (the "species redundancy" hypothesis; Lawton 1994, Walker 1995, Flecker 1997).

Links between diversity and ecosystem processes have been shown almost exclusively in grassland systems (Tilman and Downing 1994, Tilman et al. 1996, Hooper and Vitousek 1997, 1998) while aquatic studies linking community structure (biodiversity and species composition) to ecosystem processes are rare (Vitt and Chee 1990, Finlay et al. 1997). Here we report on an experiment conducted in summer 1998, where we manipulated species richness of 5 species of submersed aquatic macrophytes (*Potamogeton pectinatus*, *Potamogeton nodosus*, *Potamogeton crispus*, *Zannichellia palustris*, and *Ruppia maritima*) to measure the effect of macrophyte species richness and individual species on final community biomass and the resilience of this biomass after a clipping disturbance. This research is crucial in the effective management, conservation, and restoration of wetlands because wetland ecosystem functioning and sustainability may ultimately be dependent on wetland species composition and diversity of submersed aquatic macrophytes.

MATERIALS AND METHODS

In summer 1998, we created 204 mesocosm wetlands (1.5 m diameter, 0.5 m high) which were filled half with terrestrial soil and half with stream water. Terrestrial soil was used to minimize germination of seeds adapted to saturated

environments. A drip irrigation system was connected to a source of stream water which ensured that inflow (2 l/h) always exceeded evaporation rates. Basic water chemistry on the inflow and outflow of the mesocosms was measured using standard analytical protocols and is reported elsewhere (Engelhardt 2000).

Sixteen "community" treatments (5 monospecific, ten 3-species, and one 5-species) consisting of 5 species of submersed aquatic macrophytes (*Potamogeton pectinatus* L., *Potamogeton nodosus* Poir., *Potamogeton crispus* L., *Zannichellia palustris* L., and *Ruppia maritima* L.) were planted in the pools in mid-June 1998. The above species were selected for the experiment because they are the most abundant submersed vascular plant species occurring in freshwater marshes near the Great Salt Lake, Utah (Cox and Kadlec 1995). *Potamogeton pectinatus* tubers were bought from a nursery in Wisconsin (Kester's Wild Game Food Nurseries, Inc., Omro, WI), the source of *P. nodosus* shoots was a pond complex in Texas, of *P. crispus* shoots was a pond in Utah, of *Z. palustris* shoots was a stream in California, and of *Ruppia maritima* was a Chesapeake Bay tributary in Maryland. The community treatments received 20-21 individuals per pool (21 individuals in the mono- and tri-specific communities, 20 individuals in the 5-species community). Pools for each treatment were chosen randomly. Twelve replicates of each mono- and tri-specific community treatment were planted. Twenty-four replicates were planted for the five-species community. Templates were used for planting to ensure consistent densities and spacing per pool. The plants in the 3-species communities were planted such that any one species was surrounded by the other two species but not by individuals of its own species. We planted the five-species communities in four rows, each row containing one individual of each species. Planting order in a row was consistent within a pool but not among pools. Any one individual was surrounded by individuals of the other species only.

At the end of July 1998, we clipped all above-ground vegetation at the sediment surface in half of the pools for each treatment to simulate a wetland drawdown to a mudflat (the above ground vegetation dies but the roots survive). The pools were clipped again at the end of the growing season in early October. The vegetation was dried at 60°C for 3 to 5 days and subsequently weighed. Total ecosystem respiration, which is the sum of respiration by macrophytes, algae, invertebrates, and microbes, was measured in all pools before the clipping disturbance and once per week for 6 weeks after the disturbance using Orion (Model 810) dissolved oxygen meters. Dissolved oxygen concentrations were measured in the middle of each pool and about 4 cm below the water surface when oxygen concentrations were highest (2 hours before dusk) and again at dawn when oxygen concentrations were lowest. The drip irrigation system was turned off before the evening measurement and turned back on after the morning measurement to eliminate oxygen introduction during the night. Total ecosystem respiration was calculated as the difference between the dusk and dawn measurements, assuming the oxygen lost from the water surface or floating leaves to the atmosphere was close to zero. Macrophyte above-ground biomass and ecosystem respiration were moderately correlated (Pearson Correlation Coefficient; $r = 0.47$, $P < 0.001$) and were analyzed as two separate variables.

RESULTS AND DISCUSSION

Species richness had a positive effect on above-ground biomass (2-way ANOVA; $F_2 = 2.66$, $P = 0.07$) in control (Figure 1A) and clipped (Figure 1B) pools, where maximum biomass stayed the same in all diversity treatments, but minimum biomass increased as species richness increased. This pattern is consistent with a sampling effect (Tilman et al. 1997, Tilman 1999) which suggests that the probability increases as species are added to a community that a superior competitor is present in the community. Superior competitors are typically productive; hence productivity increases when a superior competitor is added. *Potamogeton pectinatus* produced the most biomass (Figure 1A) and is the most competitive species in our mesocosm systems (Engelhardt 2000, Ritchie and Engelhardt 2001). *Zannichellia palustris* and *R. maritima*, on the other hand, were not productive, suggesting that when *P. pectinatus* is added to communities containing *Z. palustris* and *R. maritima*, total community biomass should increase. Thus, the diversity-productivity hypothesis (Naeem et al. 1994, 1995, 1996, Tilman et al. 1996, Jolliffe 1997) is supported by our data.

Even though productivity increased with increasing species richness, the interaction between clipping and species

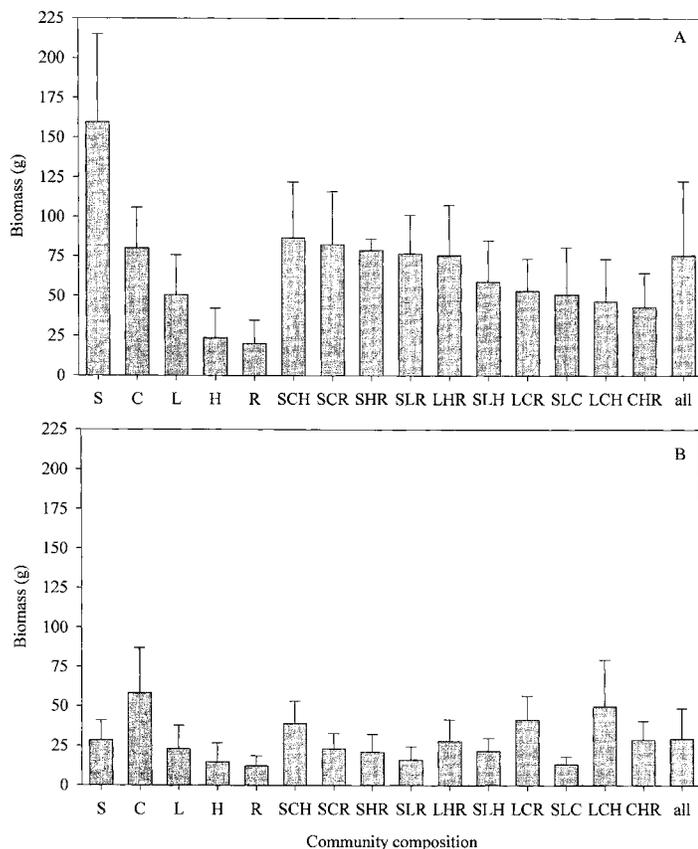


Figure 1. Total above-ground biomass per mesocosm (mean \pm 1 std) of the 16 community treatments in control (A) and clipped (B) pools harvested in early October 1998. S, *Potamogeton pectinatus*; L, *Potamogeton nodosus*; C, *Potamogeton crispus*; H, *Zannichellia palustris*; R, *Ruppia maritima*. The 16 communities consisted of all possible combinations of one, three, and five (ALL) species.

richness was not significant (2-way ANOVA; $F_2 = 0.11$, $P = 0.90$). Similarly, ecosystem respiration was not affected over time by diversity (repeated measures ANOVA; Wilks Lambda $F_{16,370} = 1.41$, $P = 0.13$), and the interaction between clipping and diversity was not significant over time (repeated measures ANOVA; Wilks Lambda $F_{16,370} = 0.98$, $P = 0.48$). The interaction between time and clipping, however, was significant (Wilks Lambda $F_{8,185} = 3.29$, $P = 0.002$). We conclude that resilience (defined as recovery to the control level after the clipping disturbance; Pimm 1984, Tilman and Downing 1994) of above-ground biomass and ecosystem respiration was not mediated by diversity, i.e., diversity did not affect recovery of wetland above ground biomass and ecosystem respiration after clipping. We therefore have to reject the diversity-stability hypothesis (McNaughton 1977, Pimm 1984, Berish and Ewel 1988, Vitousek and Hooper 1993) at this time.

In contrast to diversity, the presence or absence of *P. pectinatus* and *P. crispus* significantly affected total above-ground biomass (Figure 1A, B; 6-way ANOVA; $P = 0.001$ ($F_1 = 6.87$) and $P = 0.006$ ($F_1 = 7.72$), respectively). As mentioned above, *P. pectinatus* had a positive effect ($P < 0.05$) on system biomass when it was present in the community. In contrast, *P. crispus* had significant negative effect on total system biomass. Even though *P. crispus* is a productive species in monoculture, it suffers under interspecific competition when in mixed culture (Engelhardt and Ritchie 2001). Thus, this species produces less in mixed culture and therefore lowers average productivity of the entire community.

Interactions between clipping and biomass were significant when *P. pectinatus* and *P. crispus* were present in the community (6-way ANOVA; $P < 0.001$ ($F_1 = 13.53$) and $P = 0.05$ ($F_1 = 3.90$), respectively). Thus, *P. pectinatus* and *P. crispus* significantly affected the response of the wetland mesocosms to clipping; however, the two species generated opposing responses. *Potamogeton pectinatus* pools did not grow well after clipping, whereas *P. crispus* pools significantly increased in biomass in the clipped pools relative to the control pools. These trends suggest that the presence of *P. pectinatus* in a system decreases system resilience to disturbance. *Potamogeton crispus*, on the other hand, is a disturbance-tolerant species (Sabbatini and Murphy 1996) and may therefore increase resilience of ecosystem biomass to disturbance. This may explain the lack of a diversity-stability relationship because the best competitor and most productive species (*P. pectinatus*) decreased the resilience of the system, whereas the opposite is true for *P. crispus*. The apparent absence of an observable relationship between diversity of submersed aquatic macrophytes and resilience requires further study.

Total ecosystem respiration was significantly affected over time by the presence of *P. pectinatus* (repeated measures ANOVA; Wilks Lambda $F_{8,179} = 4.46$, $P < 0.001$), *P. nodosus* (repeated measures ANOVA; Wilks Lambda $F_{8,179} = 4.20$, $P < 0.001$), and *R. maritima* (repeated measures ANOVA; Wilks Lambda $F_{8,179} = 2.11$, $P = 0.04$). Similarly, the resilience of total ecosystem respiration was affected by the presence of certain macrophyte species (Figure 2A-E). Ecosystem respiration recovered within 4 days after clipping when *Z. palustris* was present in the community. The presence of *P. nodosus* allowed recovery within 11 day, followed by the presence of *P. crispus* with a 39 day recovery period. Presence of *P. pectinatus* and

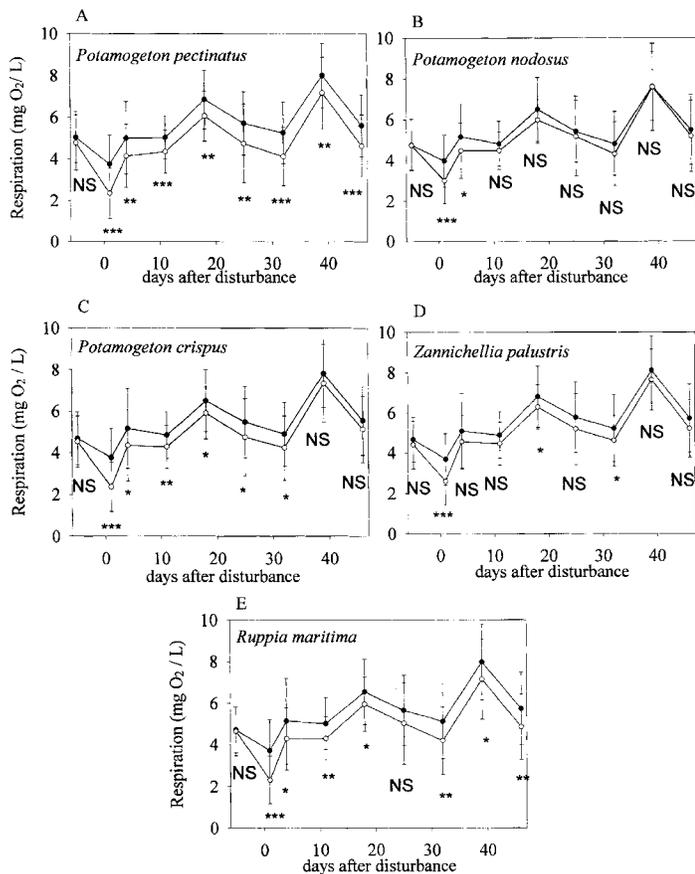


Figure 2. Resilience of total ecosystem respiration (mean \pm 1 std) when *P. pectinatus* is present (A), *P. nodosus* is present (B), *P. crispus* is present (C), *Z. palustris* is present (D), and *R. maritima* is present (E) in the community. Closed circles are control pools and open circles are clipped pools. NS indicates no significance, * is significant at $\alpha < 0.05$, ** is significant at $\alpha < 0.01$, and *** is significant at $\alpha < 0.001$.

R. maritima did not allow the recovery of ecosystem respiration by the end of the study period. These results suggest that the presence of *Z. palustris* and *P. nodosus* can increase the resilience of wetland ecosystems by decreasing the recovery time of total ecosystem metabolism.

Species richness of submersed aquatic macrophytes apparently could not explain the respiration differences in the created wetland systems, nor the differences in resilience of biomass and respiration to simulation of one important aspect of drought: death of above-ground plant parts. We found significant effects between specific species and ecosystem processes, and each of the five macrophyte species in our study had non-redundant effects on either above-ground biomass (*P. pectinatus* and *P. crispus*), the recovery of biomass after the disturbance (*P. crispus*), total ecosystem respiration (*P. pectinatus*, *P. nodosus*, and *R. maritima*), and/or the recovery of respiration (*P. nodosus* and *Z. palustris*). Thus, we reject the diversity-redundancy hypothesis because particular species had unique, dominant effects. This means that diversity is indeed important in multidimensional space, because different species fulfilled different roles in the system attributes we measured.

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