Journal of Ecology

British Ecological Society

Journal of Ecology doi: 10.1111/j.1365-2745.2009.01603.x

Diversity enhances community recovery, but not resistance, after drought

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Summary

1. There is growing concern that the current loss of biodiversity may negatively affect ecosystem functioning and stability. Although it has been shown that species loss may reduce biomass production and increase temporal variability, experimental evidence that species loss affects ecosystem resistance and resilience after perturbation is limited.

2. Here, we use the response of experimental plant communities – which differ in diversity – to a natural drought to disentangle the effects of diversity and biomass on resistance, recovery and resilience.

3. Resistance to drought decreased with diversity, but this pattern was highly dependent upon pre-drought biomass. When corrected for biomass, no relationship between diversity and resistance was observed: at each level of diversity, biomass production was reduced by approximately 30%.

4. In contrast, recovery (change in biomass production after drought) increased with diversity and was independent of biomass. Resilience (measured as the ratio of post- to pre-drought biomass) was similar at each level of diversity.

5. *Synthesis*. On the one hand, our results confirm earlier findings that a positive relationship between diversity and resistance is mainly driven by pre-perturbation performance rather than by diversity. However, the results also show that recovery after drought strongly increased with diversity, independent of performance. We conclude that it is this diversity-dependent recovery which allowed diverse, productive communities to reach the same level of resilience as less diverse (and productive) communities. This finding provides strong experimental evidence for the insurance hypothesis.

Key-words: biodiversity, drought, ecosystem functioning, insurance hypothesis, resilience, stability

Introduction

In the last decade, progress has been made in understanding the role of biodiversity in ecosystem functioning. Several experiments have shown a positive relationship between plant diversity and above-ground biomass production (Hector *et al.* 1999; Tilman *et al.* 2001; Roscher *et al.* 2005; van Ruijven & Berendse 2005; Spehn *et al.* 2005). Detailed analysis in some of these experiments has also shown that the inter-annual variability of the above-ground biomass production, which can be used as a measure of stability, decreases with diversity (Tilman, Reich & Knops 2006; van Ruijven & Berendse 2007; Flynn *et al.* 2008; Isbell, Polley & Wilsey 2009). A positive relationship between diversity and the stability of community properties has also been found in other experiments (Cottingham, Brown & Lennon 2001; Loreau *et al.* 2002). Other aspects of stability, however, have remained more obscure. In the light of climate change, the response of ecosystems to perturbations, such as drought, is particularly important. Ecosystems may resist change in functioning under perturbation and/or show resilience by returning to the original state after perturbation. The insurance hypothesis predicts that both resistance and resilience should increase with diversity (Yachi & Loreau 1999). The hypothesis is based on the assumption that species differ in their response to environmental change. Thus, as species richness increases, the range of species responses will increase. Consequently, more diverse communities have a higher chance of including a species that will increase its performance and compensate for other species in response to perturbation. However, this hypothesis should be tested using rigorous experimental studies (Loreau *et al.* 2001). Several experiments have been

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devoted to the resistance to drought in grassland communities, but the results are conflicting. This appears to be related to the relationship between diversity and above-ground biomass, the latter of which is also used to determine resistance. Resistance to an experimental drought declined with diversity, when diversity and biomass were positively correlated (Pfisterer & Schmid 2002; van Peer *et al*. 2004; De Boeck *et al*. 2008), but increased with diversity when the initial relationship between diversity and biomass was negative (Tilman & Downing 1994). In natural grasslands in which diversity and biomass were not related, diversity did not affect resistance (Kahmen, Perner & Buchmann 2005). This led a recent study to conclude that pre-drought biomass, rather than diversity, determines resistance (Wang, Yu & Wang 2007), but diversity and biomass were not related in their study.

The relationship between diversity and resilience is more obscure, as most of the studies that addressed resistance to drought did not investigate the recovery of the communities after drought. In one experimental study, resilience (measured as post- to pre-drought biomass ratios) was higher at low diversity after 9 months, but unaffected by diversity after 1 year (Pfisterer & Schmid 2002). In contrast, plant diversity was found to increase below-ground productivity in response to simulated drought, which may have increased above-ground resilience, but this was not measured (Kahmen, Perner & Buchmann 2005). Here, we analyse the effects of a natural drought on community biomass in a long-term biodiversity experiment to test the insurance hypothesis.

Materials and methods

EXPERIMENTAL DESIGN

The biodiversity experiment was initiated in 2000 in Wageningen, the Netherlands. We established 102 experimental plots of 1 m^2 in six replicated blocks on an arable field in early spring. Plots were 1 m apart, whereas the distance between blocks was 2 m. In each plot, the topsoil was removed to a depth of 45 cm. At this depth, the mineral sand layer below the arable field soil was reached. Wooden frames measuring $1 \times 1 \times 0.5$ m ($l \times w \times h$) were placed in each hole and filled with a mixture of pure sand and soil from an old field (3 : 1). Seeds were sown on the same soil mixture in plug trays in the glasshouse. After 3 weeks, the seedlings were planted. In total, 144 seedlings were planted per plot in a substitutive design (i.e. identical total seedling density in each plot). During the first 3 months, plots were watered regularly to avoid desiccation of the seedlings. After this period, no additional watering was applied.

Species were selected from a pool of four grass species (*Agrostis capillaris* L., *Anthoxanthum odoratum* L., *Festuca rubra* L., *Holcus lanatus* L.) and four dicot species (*Centaurea jacea* L., *Leucanthemum vulgare* Lamk., *Plantago lanceolata* L., *Rumex acetosa* L.). Nomenclature follows van der Meijden (1990). Species will be referred to by their genus names. All species are C_3 perennials and commonly coexist in temperate European hay meadows. Each block contained monocultures of all species, four mixtures of two and four species, and an eight-species mixture. The mixtures of two and four species were assembled by constrained random selection from the species pool. Selecting a certain composition twice was not allowed in this procedure. Composition was maintained throughout the experiment by removing seedlings of all other species at monthly intervals during each growing season (see van Ruijven, De Deyn & Berendse 2003 for details about weeding).

Above-ground primary productivity was measured by harvesting all plant material after the vegetation had reached peak standing biomass. As all above-ground tissue is newly produced each year and every species is present throughout the growing season, above-ground biomass at the end of the growing season provides a reasonable estimate of annual above-ground productivity. In early August each year, plants were clipped to 2.5 cm above the soil surface, sorted to species and dried for at least 48 h at 70 °C prior to weighing. To avoid confounding edge effects, plots were divided into a centre of 60×60 cm and a surrounding edge. Only data from the centres were used for the analysis. This analysis is based on data of above-ground biomass from 2005 to 2007.

Summer heatwaves can have profound negative effects on productivity. Detailed analysis of an earlier heatwave in Europe revealed that the observed drop in productivity is mainly caused by drought stress (water limitation), rather than high temperatures (Reichstein *et al*. 2007). The impact of the summer heatwave of 2006 was particularly strong in this experiment, because it occurred during the last 2 months of the growing season before the annual harvest of the experiment. Characteristics of the heatwave are shown in Fig. 1. The total rainfall during this period was only 47 mm, whereas the long-term average in the Netherlands is 140 mm. These climate data were obtained from the meteorological station in Wageningen, located approximately 2 km from the experimental site. However, the characteristics of the heatwave were very similar throughout the country. 19 July 2006 was the warmest day in July in over 300 years in the Netherlands (KNMI 2009).

CALCULATIONS AND STATISTICAL ANALYSIS

Resistance is the ability to withstand perturbation. It was determined as the change in biomass as a result of the drought and calculated as the difference in biomass between the year of the drought (2006) and the year before the drought (2005). To account for the effect of pre-drought productivity, we also calculated proportional resistance as the difference in logs of drought and pre-drought biomass. Similar to our measure of resistance, we determined recovery as the change in

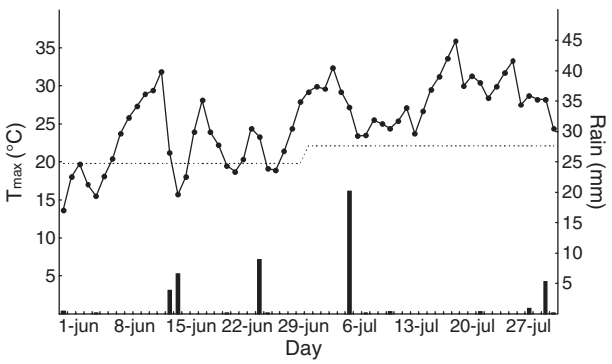


Fig. 1. Daily maximum temperature (line) and rainfall (bars) in Wageningen, the Netherlands in June and July 2006. The long-term average T_{max} for both months (over the last 30 years) is shown as a dotted line. Total rainfall in this period was only 47 mm, whereas the long-term average rainfall for these 2 months is 140 mm.

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biomass after drought. It was calculated as the difference in biomass between the post-drought year (2007) and the year of the drought (2006). Proportional recovery was calculated as the difference in logs of post-drought and drought biomass. Resilience is usually calculated as the ratio of post-drought (2007) to pre-drought (2005) biomass. As such, it combines resistance and recovery and provides a measure of the extent to which biomass production after drought has recovered to the pre-drought level. Resistance, recovery and resilience measures were also calculated for individual species.

Since the drought occurred naturally, a true control treatment is lacking. However, the drought occurred during the seventh year of the experiment. At that time, the relationship between productivity and species richness observed in the experiment, which varied substantially with time during the first years of the experiment, had stabilized at a strongly positive level (van Ruijven & Berendse 2009). In addition, the analysis for individual species was restricted to plots in which a given species' biomass in a given year was at least 10% of the mean plot biomass in the same year, because very small populations are prone to substantial year-to-year variation (Waltho & Kolasa 1994), which may lead to wrong conclusions about the effects of drought.

In the analyses described below, diversity refers to the number of species in the plots. Since the realized richness in the 3 years under study was almost identical to the planned richness values (1.99 ± 0.01, 3.89 ± 0.03 and 7.50 ± 0.19 for two, four and eight-species mixtures, respectively) and using realized richness did not affect the results, we decided to use the planned richness values here.

The effect of time on biomass was determined using repeated-measures Generalized Linear Models (GLM) with year as the within-subjects factor, block as between-subjects factor and diversity as covariate. In this procedure, pairwise comparisons were used to compare the 3 years. Relationships between diversity and biomass, resistance, recovery and resilience were determined using GLM with block as a random factor and the logarithm (using 2 as the base) of species richness as covariate. To provide a statistical basis for the dependency of absolute resistance and resilience upon pre-drought biomass, the latter was included as a covariate in the GLM described above, fitting it before diversity using sequential (type I) sums of squares. Data were natural log-transformed when necessary to meet assumptions of normality.

Results

Overall, biomass differed strongly between years ($F_{2,194} = 30.6$; $P < 0.001$). Biomass was significantly lower during the drought than in 2005 and 2007 ($P < 0.05$), but the relationship between diversity and biomass was positive in each year. The slope of the relationship showed a small reduction during the drought, but this difference was not significant ($P > 0.05$).

Resistance decreased with diversity (Fig. 2a; $F_{1,95} = 11.8$, $P < 0.001$). When pre-drought biomass was included in the model, it showed a strong negative relationship with resistance ($F_{1,94} = 57.1$, $P < 0.001$) and the negative effect of diversity disappeared. Indeed, proportional resistance showed no relationship with diversity (Fig 2b; $F_{1,95} = 1.6$, $P = 0.22$). The overall reduction in biomass as a result of the drought was 33%.

Recovery, i.e. the biomass difference post-drought minus drought, increased with diversity (Fig. 2c; $F_{1,95} = 4.2$, $P < 0.05$), but showed no relationship with pre-drought biomass ($F_{1,94} = 0.3$, $P = 0.57$). Proportional recovery showed a similar increase with diversity (Fig. 2d; $F_{1,95} = 4.5$, $P < 0.05$).

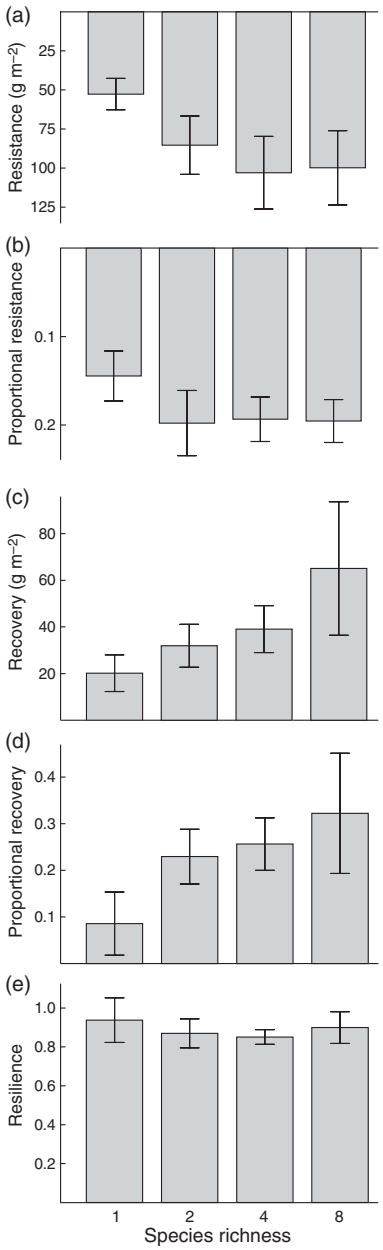


Fig. 2. Diversity significantly decreased (a) absolute resistance (g m^{-2}), but this was a function of biomass as diversity had no effect on (b) proportional resistance. Diversity had a strong positive effect on (c) recovery (g m^{-2}), but in contrast to resistance, this pattern was not driven by biomass differences and (d) proportional recovery also increased with diversity. As a consequence of these resistance and recovery patterns, resilience (e) was similar at each level of diversity. Bars show means ± SE.

Resilience, measured as the ratio between post-drought and pre-drought biomass, was not affected by diversity (Fig. 2e; $F_{1,95} = 0.3$, $P = 0.44$). One year after the drought (2007), biomass was on average 90% of pre-drought biomass.

Similar to the community, resistance of most species was highly dependent upon pre-drought biomass ($P < 0.05$).

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Diversity did not affect absolute ($P \geq 0.25$) or proportional resistance ($P \geq 0.19$; see Fig. 3a,b for one species). The results for two low-biomass species, *Leucanthemum* and *Rumex*, were slightly different. For these species, resistance was not different from zero ($P > 0.05$) and independent of pre-drought biomass ($P \geq 0.12$) and diversity ($P \geq 0.70$).

Most species showed no effects of diversity on recovery ($P \geq 0.32$), but for one species (*Anthoxanthum*), recovery strongly increased with diversity (Fig. 3c; $F_{1,22} = 9.2$, $P < 0.01$). Similar to the community, pre-drought biomass did not affect recovery of any species ($P \geq 0.35$). Proportional recovery of *Anthoxanthum* also increased with diversity (Fig. 3d; $F_{1,22} = 16.2$, $P < 0.001$).

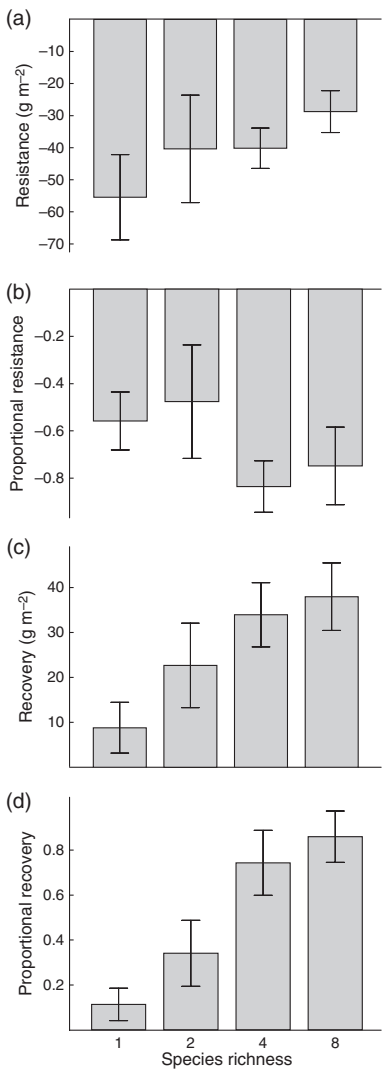


Fig. 3. Resistance to and recovery from drought for the grass species *Anthoxanthum odoratum* at different levels of diversity. Absolute resistance (a) appeared to increase with diversity, but this was not significant. Instead, resistance was a function of pre-drought biomass and proportional resistance (b) was not affected by diversity. In contrast, recovery (c) strongly increased with diversity. This pattern was independent of biomass and proportional recovery (d) also strongly increased with diversity. Bars show means ± SE.

On average, resilience of most species was not different from 1 (100%), indicating post-drought biomass was similar to pre-drought biomass. Two species (*Anthoxanthum* and *Centaurea*) showed resilience smaller than 1 ($P < 0.05$). Most species showed no relationship between diversity and resilience, but *Anthoxanthum* showed a positive relationship ($F_{1,22} = 6.1$, $P < 0.05$). Resilience of this species was less than 1 at low diversity, but greater than 1 at higher levels of diversity.

Discussion

RESISTANCE

Our analysis clearly shows that the negative relationship between diversity and resistance, as observed in our experiment and other studies (Pfisterer & Schmid 2002; De Boeck *et al.* 2008), is mainly caused by differences in pre-drought biomass. Productive plots, which were also more diverse, showed decreased resistance compared with less productive low-diversity plots. Individual species showed very similar patterns. These findings confirm the suggestion by Wang, Yu & Wang (2007) that initial productivity, rather than diversity, determines community resistance. The same conclusion was reached by Huston (1997) after re-analysing the positive relationship between diversity and resistance along a gradient of nitrogen addition reported by Tilman & Downing (1994). Obviously, absolute resistance and pre-drought biomass are correlated: a reduction in biomass of 200–400 g m^{-2}, as shown by some productive plots in our experiment, is impossible when pre-drought biomass is less than 200 g m^{-2}. Hence, the relationship between pre-drought biomass and resistance should be considered a statistical artefact. When corrected for pre-drought biomass, proportional resistance was similar for low- and high-productivity plots. This was also found in another diversity experiment (Pfisterer & Schmid 2002). In contrast, large differences in proportional resistance to the same drought have been observed when comparing grasslands that differed in productivity (Lepš, Osbornová-Kosinová & Rejmánek 1982; MacGillivray, Grime & Team 1995; Grime *et al.* 2000). This inconsistency is probably caused by the fact that the communities within diversity experiments share the same species pool, whereas the grasslands compared in the field studies differed strongly in species composition. Species vary widely in their resistance to drought. In addition, resistance appears to be negatively correlated to productivity via life-history strategies: species adapted to low-productivity environments typically have traits that promote resistance (Lepš, Osbornová-Kosinová & Rejmánek 1982; Lambers & Poorter 1992; MacGillivray, Grime & Team 1995).

Differences in proportional resistance between communities in a diversity experiment could arise if drought-tolerant species would become dominant. As such species have a higher chance to be included in more diverse communities; this could result in a positive relationship between diversity and resistance. Our data do not support this, probably because a single drought episode is unlikely to lead to such strong shifts in abundance of particular plant species within one growing

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season. However, such shifts can occur if the drought persists for several growing seasons (e.g. because of climate warming). A recent study in which drought stress was increased by elevated temperatures showed that water-efficient species became dominant (De Boeck *et al.* 2006).

RECOVERY AND RESILIENCE

Although resilience, measured as the ratio of post-drought to pre-drought biomass, was not affected by diversity, recovery (i.e. the increase in biomass after the drought) strongly increased with diversity. Obviously, this could already be predicted based on the negative relationship between diversity and resistance, and the neutral relationship between resilience and diversity. It suggests that communities characterized by high pre-drought biomass increased more in biomass after the drought, a pattern which was also observed when comparing grasslands that differ in productivity (Lepš, Osbornová-Kosinová & Rejmánek 1982; MacGillivray, Grime & Team 1995). Interestingly, however, this is not the case. Pre-drought biomass was a poor predictor of recovery in our study. Instead, recovery is determined by diversity: more diverse plots increased more in biomass after drought, resulting in a positive relationship between diversity and both absolute and proportional recovery.

Analyses of the individual species revealed that the positive relationship between diversity and recovery could largely be attributed to a single species, the grass *Anthoxanthum*. In contrast to the other individual species, it showed a positive relationship between diversity and recovery. This response was strong enough to also enhance resilience, which increased from only 67% in monocultures to 111% at the highest level of diversity. When comparing the recovery of *Anthoxanthum* (Fig. 3c) and the communities (Fig. 2c), it becomes clear that this particular species is responsible for almost 60% of the recovery at high diversity. It is not entirely clear what may have caused this species' response. The fact that its recovery was low in monoculture but increased with diversity suggests that this species is superior at expanding after the disturbance caused by the drought. The observation that this grass species generally forms dense root mats in the upper soil layer (J. van Ruijven, pers. obs.), which generally is most affected by drought, may support this hypothesis. To test if this species profits from the presence of other species, we performed additional analyses in which the presence of other species was included as a covariate after fitting block and diversity. This revealed that both diversity ($F_{1,25} = 9.6$; $P < 0.01$) and the presence of the dominant species, *Centaurea* ($F_{1,25} = 6.4$; $P < 0.05$), enhanced the recovery of *Anthoxanthum* (Fig. 4). The positive effect of *Centaurea* appears to decrease with its abundance (i.e. with increasing diversity), but we could not adequately test this because of lack of replication at the level of two species and lack of plots without *Centaurea* at the highest level of diversity. Interestingly, recovery and resilience of *Centaurea* were independent of diversity, indicating the expansion of *Anthoxanthum* after the drought did not affect the performance of the dominant species.

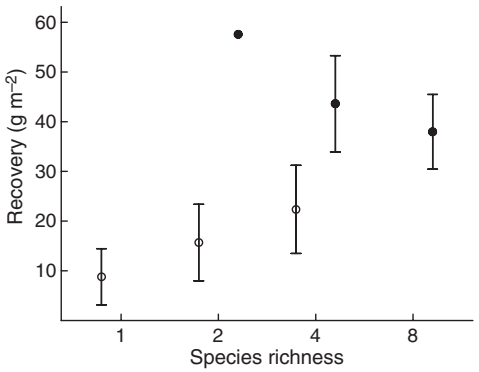


Fig. 4. The relationship between diversity and recovery of *Anthoxanthum odoratum*, as shown in Fig. 3c, split into plots with (closed dots) and without (open dots) the dominant species in the experiment, *Centaurea jacea*. Diversity had an overall positive effect on recovery, but the presence of *Centaurea* further enhanced it.

Although a single species appears to be responsible for community recovery, it should be noted that this is not a typical selection effect. In general, a positive selection effect occurs when a species, which has a strong positive effect on a given ecosystem process in monoculture, dominates the mixtures. In this case, however, resilience of *Anthoxanthum* was below average in monoculture and it only showed high recovery, leading to post-drought biomass exceeding pre-drought biomass, in diverse mixtures. In addition, even in the post-drought year it did not strongly dominate mixtures: its mean relative abundance in 2007 was only 28% (ranging from 18 to 38%) in eight-species mixtures.

Conclusions

The insurance hypothesis states that diverse communities have a higher chance of including a species which will increase its performance and compensate for other species in response to perturbation (Yachi & Loreau 1999). When considering resistance to a single drought, our data show that this hypothesis has to be rejected. Diversity did not affect proportional resistance. We did find a relationship between absolute resistance and pre-drought performance: resistance decreased with increasing productivity. This is a general pattern, which has emerged from both experimental and field studies, but it should be treated with caution as a statistical artefact.

In contrast to resistance, recovery did depend on diversity, but was independent of pre-drought biomass. Although resilience was equal at each level of diversity, the results clearly show that increased recovery of biomass production after drought enabled high-diversity communities to reach the same level of resilience as less diverse communities, which suffered a far smaller reduction in biomass. Detailed analysis revealed that the increased recovery of high-diversity communities was mainly driven by a single species, which showed a positive relationship between diversity and both resilience and recovery. This finding strongly supports the insurance hypothesis, and it constitutes another argument for protecting biodiversity.

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Acknowledgements

This work was partly supported by a grant from the Dutch Organisation for Scientific Research (NWO) within the framework of the Biodiversity Programme. We are grateful to Frans Möller, Jan van Walsem, Maurits Gleichman and numerous other field workers who helped maintaining the experiment and collecting the data.

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Received 17 July 2009; accepted 13 October 2009
Handling Editor: Jason Fridley

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