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Experimental investigation of the origin of fynbos plant community structure after fire

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- *Background and aims* Species in plant communities segregate along fine-scale hydrological gradients. Although this phenomenon is not unique to fynbos, this community regenerates after fire and therefore provides an opportunity to study the ecological genesis of hydrological niche segregation.
- *Methods* Following wildfires at two field sites where we had previously mapped the vegetation and monitored the hydrology, seeds were moved experimentally in >2500 intact soil cores up and down soil-moisture gradients to test the hypothesis that hydrological niche segregation is established during the seedling phase of the life cycle. Seedling numbers and growth were then monitored and they were identified using DNA bar-coding, the first use of this technology for an experiment of this kind.
- *Key Results* At the site where niche segregation among Restionaceae had previously been found, the size of seedlings was significantly greater, the wetter the location into which they were moved, regardless of the soil moisture status of their location of origin, or of the species. Seedling weight was also significantly greater in a competition treatment where the roots of other species were excluded. No such effects were detected at the control site where niche segregation among Restionaceae was previously found to be absent.
- *Conclusions* The finding that seedling growth on hydrological gradients in the field is affected by soil moisture status and by root competition shows that hydrological niche segregation could potentially originate in the seedling stage. The methodology, applied at a larger scale and followed-through for a longer period, could be used to determine whether species are differently affected by soil moisture.

Key words: Translocation experiment, seedling regeneration, fire, soil-moisture gradient, hydrological niche, root competition, DNA bar-coding, regeneration niche.

INTRODUCTION

Plant community ecology has recently made important advances with the long-standing problem that Hutchinson (1961) characterized 50 years ago as ‘the paradox of the plankton’. This is the fundamental question of how species that compete for the same set of essential resources manage to coexist with one another in species-rich communities. The two theoretical answers to this question are that coexistence requires a stabilizing mechanism that preserves species richness by relaxing the effect of interspecific competition on rare species, or an equalizing mechanism that minimizes fitness differences between species so that the exclusion of competitively inferior species is very slow (Chesson, 2000). Niche differences between species are stabilizing, while the neutral model (Hubbell, 2001) embodies the dominant importance of an equalizing mechanism. Although it is inherently unlikely that the key assumption of the neutral model that competitors are equivalent is correct (Purves and Turnbull, 2010), it is probably common for equalizing mechanisms to make a contribution to coexistence, e.g. operating through disturbance (Huston, 1979; Laurie and Cowling, 1985; Shea *et al.*, 2004). Stabilizing and equalizing mechanisms are not mutually exclusive and one open question is their relative degree of importance in various real communities (Adler *et al.*, 2007; Cadotte, 2007; Chase and Myers, 2011).

This question has been addressed through computational experiments with models parameterized with field data. In one of the first such studies, spatial density-dependence was found to be an important stabilizing mechanism in a community of annual plants (Rees *et al.*, 1996). Levine and HilleRisLambers (2009) found that unidentified niche differences stabilized a model of a community of serpentine annual plants. Roxburgh and Wilson (2000) used a model based upon the experimentally determined pairwise competitive relationships among seven grassland species and found that this predicted the community to be unstable, though less so than predicted by a null model. Grasslands in mesic environments such as that studied by Roxburgh and Wilson are typically cut or grazed, which provides an equalizing disturbance not represented in their model. Competitive exclusion typically occurs in mesic grasslands if grazing or cutting ceases (Watt, 1957). Silvertown and Wilson (2000) used a cellular automaton model parameterized with species-specific invasion rates measured in field experiments (Silvertown *et al.*, 1994) to examine the stability of a community of perennial grasses under different grazing regimes. Intraspecific aggregation slowed competitive exclusion, but did not stabilize the

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community. However, the competitive ranks of species were different under different grazing regimes and the outcome of competition was sensitive to the geometry of the community (i.e. which species were next to each other) and could not be predicted from competitive ranks alone. Two more recent studies show that in temperate forest (Clark *et al.*, 2010) and rangeland (Adler *et al.*, 2010), niche differences among species stabilize both communities sufficiently to explain coexistence, although in neither case were the actual niche axes elucidated.

These studies show what has been suspected, but rarely demonstrated, ever since the paradox of the plankton was first stated by Hutchinson (1961): plant communities are stabilized by niche differentiation among species. However, although we can increasingly discern the signature of niche differentiation, the identity of the niche axes involved often still remains obscure (Silvertown, 2004). One exception is the niche differentiation that occurs among plants growing along soil-moisture gradients. Plants in English meadows segregate on hydrological gradients and occupy realized niches whose breadth is constrained by interspecific competition (Silvertown *et al.*, 1999). More recently, we have demonstrated that niche segregation also occurs along soil-moisture gradients in fynbos communities in the Western Cape of South Africa (Araya *et al.*, 2011) and among annuals and herbaceous perennials in Mediterranean grassland in Spain (G. García-Baquero *et al.* University of the Basque Country, Spain, unpubl. res.). Though these are only three plant community types and many have yet to be investigated, the similarity of community structure between communities that have almost no taxa in common, even at the family level, is remarkable and suggests the mechanism involved is fundamental. This fundamental inference is supported by phylogenetic analysis (Silvertown *et al.*, 1999).

The discovery of hydrological niche separation in fynbos is perhaps surprising because these communities burn on a 15–50 year cycle, regenerating naturally after fire, and one might expect this disturbance to override any fine-scale hydrological influence. Fire may provide both equalizing and stabilizing influences upon fynbos community structure (Cowling, 1987; Bond and van Wilgen, 1995; Miller and Chesson, 2009). However, having established that plants in fynbos do segregate on soil-moisture gradients, the fact that the communities regenerate after fire provides us with a perfect opportunity to test how the pattern of hydrological niche separation originates. Fire and smoke are primers of seed germination in many fynbos species (Brown and Botha, 2004), so fires are followed by a flush of seed germination. The seedling stage is the most vulnerable in a plant's life history, when it is most prone to drought, competition, herbivory and disease. We therefore advanced the hypothesis that hydrological niche segregation among fynbos plants is initiated at the seedling stage by differential survival and growth along the soil-moisture gradient. Since in meadows interspecific competition significantly increases the niche differences among species, we proposed that the same might happen in fynbos. We tested these predictions with a soil translocation experiment performed in the field, after fire and before seed germination had started. We applied a competition treatment in the root zone, reasoning that in post-fire conditions where canopy cover is low and in the highly nutrient-poor soils of fynbos, root competition would be more important than shoot competition. We then monitored seedling numbers and growth and identified them using DNA bar-coding (Lahaye *et al.*, 2008), the first use of this technology for an experiment of this kind.

The four specific questions that we address are: (1) was seedling performance (growth or mortality) influenced by location on the soil-moisture gradient? (2) was seedling performance influenced by root competition? (3) did any effects detected in questions 1 and 2 vary between species? (4) did any effects detected differ between a site where Restionaceae have been shown to segregate on the soil-moisture gradient and a control site where Restionaceae did not segregate in this way?

MATERIALS AND METHODS

Field sites

Experiments were set up at each of two fynbos sites in the Western Cape soon after they were burned by wildfire in the austral summer of 2008/09. The sites were both included in an ongoing study (Araya *et al.*, 2011), as a part of which the vegetation and hydrology had been mapped before the fires occurred. The sites were at Jonkershoek (33·99333S, 18·95290 E) and Steenbras (34·19436S, 18·87056E). We focused our study on endemic species in the family Restionaceae because the family is species-rich, ubiquitous, contains many keystone species and most species in the family have been sequenced for the *matK* gene (Hardy *et al.*, 2008) which has been used for bar-coding plant taxa (Lahaye *et al.*, 2008).

Using null models of random species co-occurrence, Araya *et al.* (2011) found significant niche segregation in the entire fynbos plant community at both sites, and also among the Restionaceae as a sub-group at Steenbras, though not at Jonkershoek. Jonkershoek was therefore used as a control site where we did not expect to find seedling performance responding to the soil-moisture gradient. Examples of the distribution of Restionaceae species at each site are shown in Fig. 1.

Experimental design

The following protocol was followed identically at each site, except where noted. We ranked all the locations of permanent quadrats by their mean water-table depths, as derived from a site-specific hydrological model. The ranked list of locations was then divided into three strata: the wettest third of locations, the driest third and the middle third, as determined by mean annual water-table depth (see below). The disposition of quadrats in relation to hydrology is shown in Fig. 2. Each quadrat was treated as a block, with two complete replicates of the experimental treatmets in the north and south halves of each block. Four soil cores were extracted with a 9-cm-diameter bulb planter from random locations in each block and allocated at random to one of the following four treatments: (1) control – rotated 180 ° on the vertical axis and replanted; (2) root competition treatment – as treatment 1, replanted inside a sleeve of water permeable, root-impermeable cloth (Plastok®, Birkenhead, UK) with a 52-µm mesh that allowed free movement of water while inhibiting the passage of roots

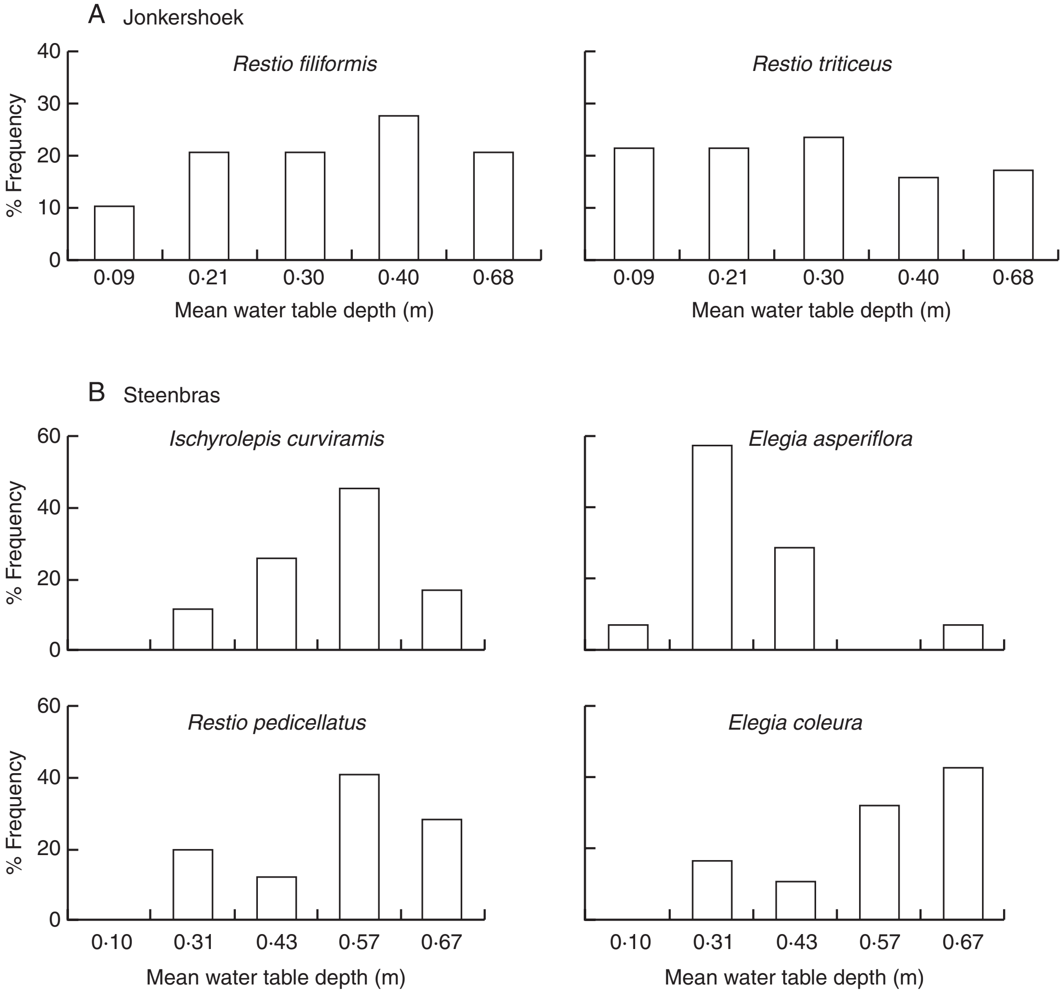

FIG. 1. Results of Araya *et al.* (2011) showing the distribution, along gradients of water-table depth, of representative species of Restionaceae in the vegetation before it was burned within our plots at (A) Jonkershoek and (B) Steenbras, Western Cape, South Africa. Significant niche segregation was present among Restionaceae at Steenbras, but not at the Jonkershoek control site (data not shown).

(Araya, 2005); (3) translocation treatment – replanted in the corresponding block (N/S) of another quadrat chosen from the stratified random sampling scheme; (4) translocation and root competition treatment – replanted in the same block as treatment 3, inside a root cloth sleeve. Translocated cores (treatments 3 and 4) were moved in equal numbers to each of the other two strata where they were planted in a randomly chosen block.

The experiments were set-up in March and April 2009, before any seedlings had appeared. A count of seedlings was made at the end of the winter in October 2009, but only at Jonkershoek since the Steenbras site was under water at that time. The experiments were destructively harvested in April 2010 when all seedlings were removed, counted, dried under silica gel and weighed. The dried seedlings were separated into morphotypes based upon visible features and a representative sample of each morphotype was bar-coded.

Hydrology

Conditions in each quadrat were derived from site-specific hydrological models based upon field measurements of water-table depth made by a combination of instrumented dip wells and fortnightly manual monitoring (for details, see Araya *et al.*, 2011). Measurements were made from October 2007 until the fire in March 2009 at Jonkershoek and from October 2006 until the fire in December 2008 at Steenbras. Mean water-table depth during the year can be used as a summary variable (e.g. in Fig. 1), but more information is contained in sum exceedance values (SEV) that measure the duration of aeration stress due to waterlogging (SEVa) and the duration of drought stress (SEVd) endured by plants over a year (Fig. 2.).

Bar-coding

Total DNA was extracted from silica gel-dried culms using the Fast DNA Spin Kit (MPBiomedicals) and the Fast Prep-24 machine for powdering the material. DNA was dissolved in 70 µL ddH$_2$O. The used amount of plant material was between 8 and 13 mg. DNA quality was checked with the NanoDrop Spectrophotometer ND-1000. Total DNA was diluted 1 : 10 with H$_2$O for the PCR-amplification.

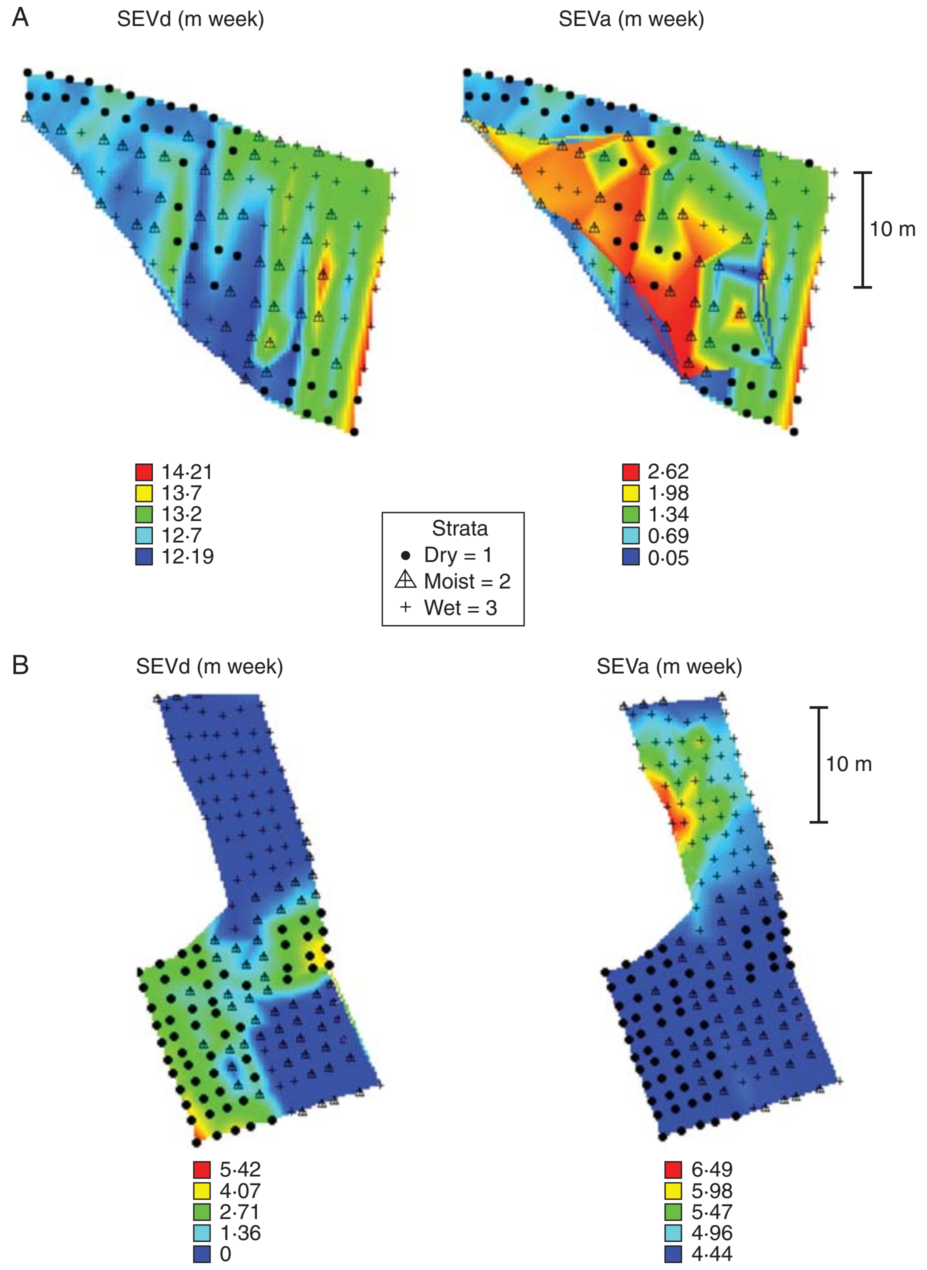

FIG. 2. The locations of experimental quadrats superimposed on hydrological maps of SEVa (sum exceedance value for aeration stress) and SEVd (sum exceedance value for drought stress) at (A) Jonkershoek and (B) Steenbras. The maps were created from a hydrological model parameterized with field data.

PCR-amplification of the *matK* plus the flanking *trnK* intron (Hilu and Liang, 1997) used the primers described in the paper of Hardy and Linder (2005). Amplification reactions with the total volume of 25 µL contained 18·25 µL H_2O, 2·5 µL 10 × PCR buffer (Sigma), 2 µL MgCl (25 mM), 0·5 µL of dNTPs(10 mM), 0·5 µL of each primer (10 µM), 0·25 µL Taq-DNA polymerase (Sigma) and 1 µL of DNA template (diluted 1 : 10 in H_2O).

The cycling was preceded by a single step of 95 °C for 4 min and finished by a single step of 72 °C for 10 min. Cycling involved 94 °C for 1 min, 52 °C for 1 min and 72 °C for 1·5 min. A total of 33 cycles yielded sufficient amounts of *matK*-product. Negative controls were included to monitor the reactions. The PCR-products were tested on agarose gels and purified using the PCR-cleaning kit (Sigma).

Sequences were generated using standard methods for automated sequencing using BigDye term v3·1. Only four of the internal primers (mk_A2, mk_B4, mk_B2 and matk_f2) mentioned in Hardy and Linder (2005) were used. The external primers used for the PCR-reaction (mk_F1 and mk_R1) were not used for sequencing because of Primer Dimers. The samples were cleaned with Sephadex and run on a DNA Sequencer (3130xl Genetic Analyzer; Applied Biosystems). Contigs of the sequences were formed using the software

Sequencher 4·6. The sequences were aligned with the software MacClade 4·07 OS X. Morphospecies were tested with multiple samples and redefined. They were matched to taxonomically recognized species by using PAUP to compile a consensus tree of *matK* sequences for both known and unknown samples and assigning mophospecies to the nearest taxon known to be present in the geographic region. The reference Restionaceae *matK* sequences used were those deposited in Genbank by Hardy *et al.* (2008).

Data analysis

Although the original design of the experiment was a balanced one, seedlings did not emerge in all cores and so seedling numbers and performance (weight) were analysed using generalized linear models in R version 2·14·2 (R Development Core Team, 2010). Stepwise deletion (Crawley, 2007) was used to obtain minimally adequate models from starting formulae that contained independent variables for the root competition treatment (0/1), species and the hydrological conditions of the source and destination quadrats. Three different ways of representing the hydrological conditions were tried in different models: (1) absolute values of the sum exceedance value (Araya *et al.*, 2011) for aeration stress (SEVa) or drought stress (SEVd) of the source and destination of the core; (2) absolute values of SEVa and SEVd for the source and the difference in each SEV variable between the source and the destination quadrat; (3) the stratum, numbered from 1 (dryest) to 3 (wettest) of the source and destination quadrats.

RESULTS

Jonkershoek

When surveyed in October 2009, restio seedlings were present in 759 of the 1232 cores. Only a very few cores contained more than a single seedling, so these results were analysed as seedlings present/absent using a model with binomial errors and a logit link function. In the minimally adequate model, the only variable that influenced the presence of seedlings measured drought stress (SEVd), which was significantly, though only very slightly higher in cores where a seedling appeared ($\bar{X} = 12{\cdot}885$, s.e. $\pm$ 0·018) than in cores where no seedling was present ($\bar{X} = 12{\cdot}790$, s.e. $\pm$ 0·021).

When the experiment was harvested in April 2010, seedlings had survived in only 89 of the original 759 cores, but there were new seedlings in 51 others, indicating that some additional germination had taken place since October. In the minimally adequate model for seedling presence in April, the only significant term was for the competition treatment ($P = 0{\cdot}012$). Nine per cent of sleeved cores contained a seedling, while 14 % of unsleeved cores did so.

Since the survivors from October were so few, mortality was analysed by separate 2 × 2 contingency tables for the effect of a sleeve ($\chi^2 = 2{\cdot}099$, d.f. = 1, $P = 0{\cdot}147$) and for the effect of translocation ($\chi^2 = 3{\cdot}168$, d.f. = 1, $P = 0{\cdot}075$). Neither had an effect on seedling survival.

The harvest in April produced 138 seedlings that were assigned to ten species by bar-coding. In descending order of abundance (*n*) these were: *Restio triticeus* (56), *R. filiformis* (44), *R. curviramis* (11), *Elegia filacea* (9), *E. caespitosa* (7), *R. capensis* (5), *R. distichus* (2), *Thamnochortus lucens* (2), *E. juncea* (1) and *Staberoha banksii* (1). Because of small sample sizes, species were analysed in three taxa: *Restio triticeus* ($n = 56$), *R. filiformis* ($n = 44$) and other ($n = 38$).

The average weight (g) of seedlings harvested in April was analysed using a model with a gamma function and a reciprocal (canonical) link. Stepwise deletion from the full model did not yield any model with a significant fit.

Steenbras. Seedlings in 305 cores harvested in April 2010 were assigned to five species by bar-coding. In descending order of abundance (*n*) these were: *Restio nudiflorus* (211), *R. corneolus* (43), *R. curviramis* (24), *R. pedicillatus* (19) and *R. bolusii* (8).

In the minimally adequate models for seedling presence in April, none of the explanatory variables was significant.

Sample sizes were small for all species except *R. nudiflorus*, so the other species were combined into '*Restio* other' for analysis of average seedling weight. The minimally adequate model for average seedling weight showed highly significant (all $P < 0{\cdot}001$) effects of species, competition (sleeve) treatment and destination stratum (model 3; see Materials and methods) (Fig. 3), but contained no significant interactions. *Restio nudiflorus* seedlings were about 60 % of the weight ($\bar{X} = 0{\cdot}050$ g, s.e. $\pm$ 0·003) of the other species ($\bar{X} = 0{\cdot}083$ g, s.e. $\pm$ 0·104).

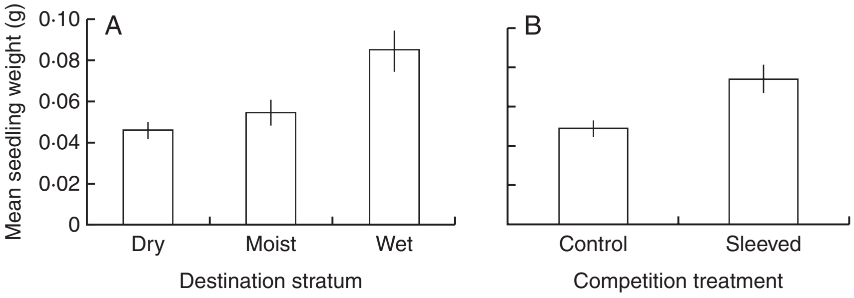

FIG. 3. Mean seedling weight ($\pm$ s.e.) in the Steenbras experiment, as affected by (A) the soil moisture stratum into which a core was translocated, and (B) the sleeve-competition treatment. No significant effects were detected in the version of this experiment conducted at Jonkershoek.

DISCUSSION

Plants in fynbos communities in the Western Cape segregate along fine-scale hydrological gradients (Fig. 1) (Araya *et al.*, 2011). This phenomenon is not unique to fynbos (Silvertown *et al.*, 1999), but because plants in fynbos regenerate after fire, the community does provide a unique opportunity to study the ecological genesis of hydrological niche segregation. Following wildfires at two field sites where we had previously mapped the vegetation and monitored the hydrology, we experimentally moved seeds in intact soil cores up and down soil-moisture gradients to answer three specific questions that would allow us to test the hypothesis that hydrological niche segregation is established during the seedling phase of the life cycle.

We tested whether seedling performance was influenced by location on the soil-moisture gradient, whether it was affected by root competition and whether species responded differently to gradient location. At Jonkershoek, the control site where niche segregation had previously been found in the fynbos community of the experimental plot, but not within the Restionaceae as a group, we failed to find any evidence that soil moisture affected growth or mortality of Restionaceae seedlings. In contrast, at Steenbras where niche segregation had been found among Restionaceae, the growth (weight) of Restionaceae seedlings was significantly greater, the wetter the location into which they were moved, regardless of the soil moisture status of their location of origin (Fig. 3A). The root exclusion treatment showed that below-ground competition reduced seedling growth by one-third (Fig. 3B). We found no difference among species in these effects, though the small sample sizes per species restricted this comparison to just two taxa. These results suggest that hydrological niche segregation among Restionaceae may orginate in the sensitivity of seedlings to soil moisture and root competition, though the crucial evidence that species are differently affected is missing.

Although the experiment involved >2500 soil cores, the sample size of seedlings and hence the statistical power of the experiment was inevitably compromised by natural variation in seed density and species and the heavy mortality typical of small-seeded species such as *Restio filiformis* and *R. triticeus* (Caddick and Linder, 2002). *Post hoc* calculation of statistical power is to be avoided in the interpretation of experimental results (Hoenig and Heisey, 2001), but it is still arguable that in this case the absence of evidence of species differences in seedling growth in relation to soil moisture should not be mistaken for evidence of absence, particularly in a short-term experiment. At Steenbras, where we should have expected to see species differences, we were only able to test for this between *Restio nudiflorus* and the other species pooled. Any heterogeneity of behaviour among the pooled species would blur the contrast with *R. nudiflorus*, making the test a weak one.

While at Jonkershoek, the most abundant seedlings (*Restio triticeus* and *R. filiformis*) belonged to species that were also recorded in the pre-burn vegetation (Fig. 1A), this was not the case at Steenbras. At this site, the most abundant seedling (*R. nudiflorus*) was not recorded in the vegetation at all. This is an example of one of the most important effects of fire on co-existence, triggering the return to the vegetation of a species that was locally rare or even absent before the burn. Such effects are widespread in fynbos (Privett *et al.*, 2001; Thuiller *et al.*, 2007) as well as in post-disturbance succession in other vegetation types (Fenner and Thompson, 2005) and, as we have found, they make it difficult to test for other processes that may be at work. Even bigger sample sizes than the ones we used are needed to penetrate the fog of history and stochasticity. A sceptic would, of course, argue that the overwhelming impact of history and stochasticity is precisely the point but, without denying this, the clear imprint of niche segregation in fynbos (Slingsby and Verboom, 2006; Araya *et al.*, 2011) and other plant communities (Cavender-Bares *et al.*, 2004; Gonzalez *et al.*, 2010) does still require explanation.

The strength of below-ground competition in inhibiting seedling growth at Steenbras was remarkable (Fig. 3B). Fynbos species, as in other fire-prone plant communities, divide between those that regenerate from seed and those that resprout. The resprouters were probably the chief source of below-ground competition for seedlings in our experiment and this should be tested in future experiments of this kind. Below-ground competition can be decisive in determing a species' hydrological niche. For example, Bartelheimer *et al.* (2010) found that, in the absence of competition, *Senecio jacobaea* would grow just as well in moist soil as dry, but when exposed to below-ground competition it grew better in the kind of dry environments where it is found in nature.

So far as we are aware, this is the first experiment of its kind to reciprocally translocate intact seed banks across a local hydrological gradient following fire with the purpose of determing how niche segregation comes about. However, reciprocal transplants between soil types or habitats are commonly used in plant ecology and evolution (Ellis and Weis, 2006; Baltzer *et al.*, 2005; Peterson-Smith and Baldwin, 2006), 'donor seed banks' are often moved from one site to another for ecological restoration (van der Valk and Pederson, 1989) and foresters use reciprocal transplants across entire geographic ranges to select the best provenances for production forestry (Campbell, 1974). We believe that the approach we have used here is a promising one, but that the fine-scale resolution needed to uncover the genesis of niche segregation within a community demands more studies.

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