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Supplementary information is available on *Nature*'s World-Wide Web site (http://www.nature.com) or as paper copy from the London editorial office of *Nature*.

Acknowledgements. This work is part of the Southern Sierra Nevada Continental Dynamics Project, supported by NSF's Continental Dynamics Program. We thank M. Ducea and J. Saleeby for permission to discuss their results before publication.

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Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity

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The functioning and stability of terrestrial ecosystems are determined by plant biodiversity and species composition[1–5]. However, the ecological mechanisms by which plant biodiversity and species composition are regulated and maintained are not well understood. These mechanisms need to be identified to ensure successful management for conservation and restoration of diverse natural ecosystems. Here we show, by using two independent, but complementary, ecological experiments, that below-ground diversity of arbuscular mycorrhizal fungi (AMF) is a major factor contributing to the maintenance of plant biodiversity and to ecosystem functioning. At low AMF diversity, the plant species composition and overall structure of microcosms that simulate European calcareous grassland fluctuate greatly when the AMF taxa that are present are changed. Plant biodiversity, nutrient capture and productivity in macrocosms that simulate North American old-fields increase significantly with increasing AMF-species richness. These results emphasize the need to protect AMF and to consider these fungi in future management practices in order to maintain diverse ecosystems. Our results also show that microbial interactions can drive ecosystem functions such as plant biodiversity, productivity and variability.

The mechanisms that control plant biodiversity are still being debated. The ability of many plant species to co-exist, and thus to determine plant biodiversity, can be explained by competitive interactions[6,7], by spatial or temporal resource partitioning[8,9], by disturbance creating new patches for colonization[10,11], and by interactions among different functional groups of organisms that constitute ecosystems[12–15]. So far, little attention has been paid to the effects of microbe–plant interactions, particularly the mycorrhizal symbiosis, on ecosystem variability, productivity and plant biodiversity. AMF are abundant in soils of most ecosystems; these fungi form mutualistic symbiotic associations with the roots of ~80% of all terrestrial plant species, thereby acting as extensions of plant root systems and increasing nutrient uptake, especially of phosphorus[16]. The presence of AMF in ecosystems increases plant biodiversity[17]. However, not only are AMF present in most ecosystems, but communities of AMF also occur, which vary in species composition, species number and, therefore, in AMF biodiversity[18,19]. Furthermore, AMF biodiversity is greatly reduced in some ecosystems[20]. Different AMF species induce differential growth responses, in terms of biomass production and clonal growth patterns, of co-existing plant species of calcareous grasslands[21,22]. On the basis of these results, we proposed that the species composition and diversity of AMF communities have the potential to determine plant biodiversity in natural ecosystems[22].

Here we show for the first time, to our knowledge, that species composition and species richness of AMF is an important contributor to plant species composition, variability, productivity and biodiversity in artificial microcosms and macrocosms.

In a greenhouse experiment (experiment 1), we compared the effects of four different native AMF taxa, which were all isolated from the soil of a calcareous grassland, and of a combination of these four AMF taxa on the species composition and structure of 48 microcosms simulating European calcareous grassland. When we compared any of these AMF treatments with the non-mycorrhizal control treatment, we found that eight of the eleven plant species were almost completely dependent on the presence of AMF to be successful in the microcosms (Fig. 1; plant species: *Brachypodium pinnatum*, *Centaurium erythrea*, *Hieracium pilosella*, *Lotus corniculatus*, *Prunella grandiflora*, *Prunella vulgaris*, *Sanguisorba officinalis* and *Trifolium pratense*). In contrast, *Carex flacca*, the only plant species of the microcosms that does not have a symbiotic relationship with AMF, had the highest biomass in the non-mycorrhizal treatment (Fig. 1f). Furthermore, the biomass produced by most of the plant species varied significantly among treatments with different single AMF taxa (Fig. 1), indicating that different plant species benefited to different extents from different AMF taxa. For example, the biomass of *Sanguisorba officinalis* and of *Trifolium pratense* was highest in microcosms inoculated with AMF A; the biomass of *Brachypodium pinnatum* was highest in microcosms containing AMF C; the biomass of *Prunella vulgaris* was highest in microcosms containing AMF D (Fig. 1e, h–j). Although altering the AMF taxa in the soil had no significant effect on the biomass of

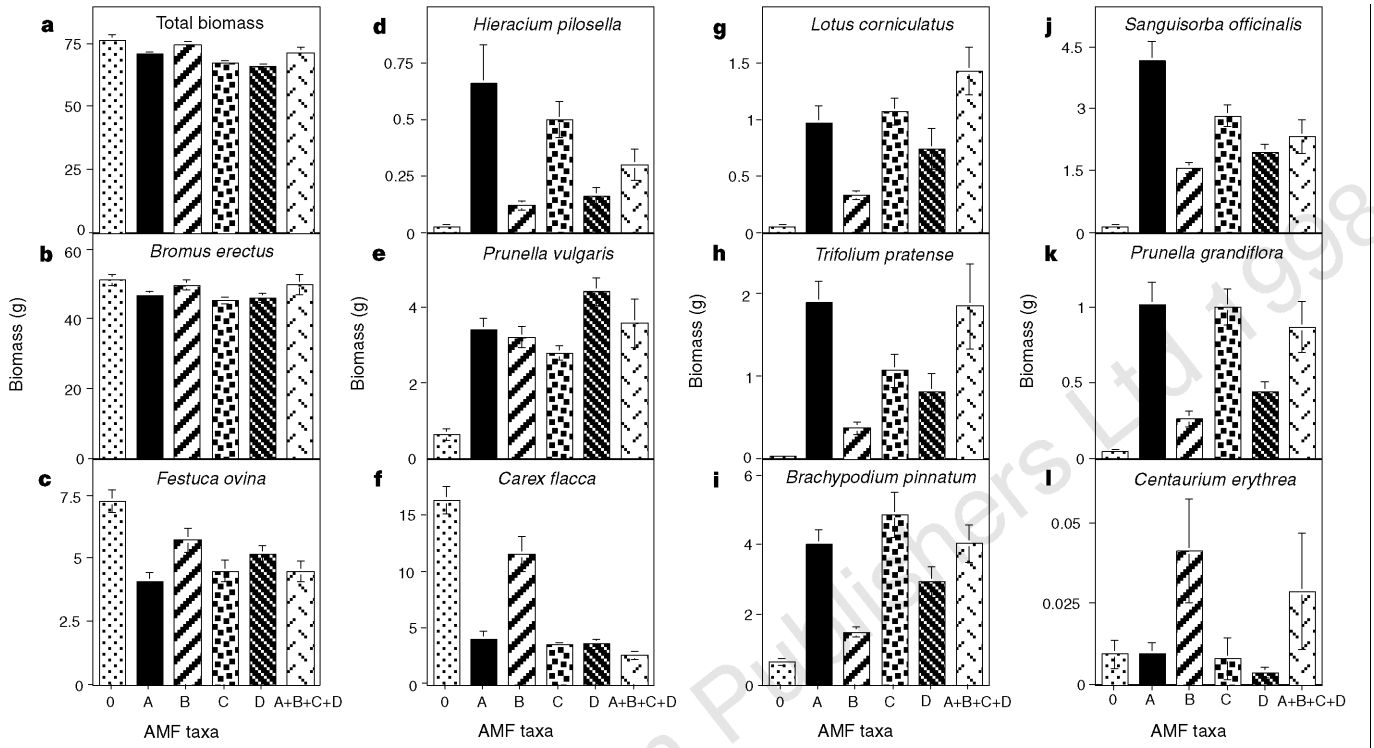

Figure 1 Above-ground biomass of individual plant species and total above-ground plant biomass (mean ± s.e.m.) in microcosms simulating calcareous grasslands, in which the composition of the AMF community was manipulated (experiment 1). Microcosms contained no AMF. (0); one of four different AMF taxa, AMF A (*Glomus* sp.; Basle, Pi), AMF B (*Glomus geosporum*; BEG 18), AMF C (*Glomus* sp.; BEG 21) or AMF D (*Glomus* sp.; BEG 19); or all four AMF taxa (AMF A+B+C+D). The biomass of most individual plant species (**c**–**k**) and the total plant biomass (**a**) differed significantly among the six treatments (ANOVA[28]; $P \leqslant 0.001$). The biomass of *Bromus erectus* (**b**) and of *Centaurium erythrea* (**l**) did not differ significantly among the treatments.

Bromus erectus, the dominant plant species in our ecosystems (Fig. 1b), the total biomass of plants in the microcosms still differed slightly, but significantly, among the AMF treatments (Fig. 1a). The biomass of several plant species in microcosms containing all four AMF taxa was roughly equal to the biomass of these plant species in those treatments that included the single AMF taxa that induced the largest growth response of the plant species (Fig. 1).

To determine whether the effects of the different AMF taxa could result in a significant alteration in the overall structure and composition of the grasslands, we used the biomass data of each of the 11 plant species as separate variables in a multivariate canonical discriminant analysis. This analysis showed that the overall structure of the plant communities varied significantly with most of the treatments with different AMF taxa (multiple analysis of variance (MANOVA) *F*-ratio for AMF treatment excluding the non-mycorrhizal treatment: $F_{44,97} = 5.06$, $P \leqslant 0.0001$).

Taken together, the results of experiment 1 show that the presence of mycorrhizal fungi is required to maintain a basic level of plant biodiversity and that, at low AMF diversity, an alteration in the composition and number of AMF taxa can lead to large fluctuations in the structure and composition of the plant community. The large changes in overall community composition were mainly manifested through a marked alteration in the biomass of subdominant species and not an alteration in the dominant grass *Bromus erectus*. The lack of a pronounced effect on *Bromus* shows that, at low AMF-species richness, changes in the community structure did not lead to marked differences in the total biomass of the microcosms. Furthermore, a reduction of AMF biodiversity from four to one AMF taxa leads to a decrease in biomass of several plant species and to a change in structure of these microcosms.

From these results, we proposed that both plant biodiversity and ecosystem productivity will increase with increasing numbers of AMF species, because of the added beneficial effect of each single AMF species. To test this hypothesis, we set up a parallel, independent field experiment at the same time that we were running experiment 1. In the field experiment, we manipulated the number of native AMF species in 70 macrocosms simulating North American old-field ecosystems (experiment 2). To ensure an unbiased test of mycorrhizal-species richness, each replicate of each treatment received randomly selected AMF species from a pool of 23 AMF, all of which were isolated from the same site. Each macrocosm received exactly the same mixture of plant seeds from 15 plant species (see Methods for plant species list). Both the plant biodiversity, as measured by Simpson's diversity index (Fig. 2a), and productivity above and below ground (Fig. 2b, c) increased with increasing AMF-species richness. The lowest plant biodiversity and productivity were found in those plots without AMF or with only a few AMF species. In contrast, plant biodiversity and productivity were highest when eight or fourteen AMF species were present. Our results show that both the productivity and the diversity of plants in a given ecosystem can be dependent on the diversity of the fungal symbionts and, therefore, suggest that AMF should be considered as determinants of plant diversity in natural ecosystems.

Our results also indicate a mechanistic explanation for the effects of mycorrhizal-species richness on productivity and plant biodiversity. Increased AMF-species richness led to a significant increase in the length of mycorrhizal hyphae in the soil (Fig. 2d), to a decreased soil phosphorus concentration (Fig. 2e) and to an increased phosphorus content in plant material (Fig. 2f). Thus, increasing AMF biodiversity resulted in more efficient exploitation of soil phosphorus and to a better use of the resources available in the system. With a design such as that of experiment 2, increasing AMF-species richness might increase the chance of including one very effective isolate. The data from experiment 1 also indicate that

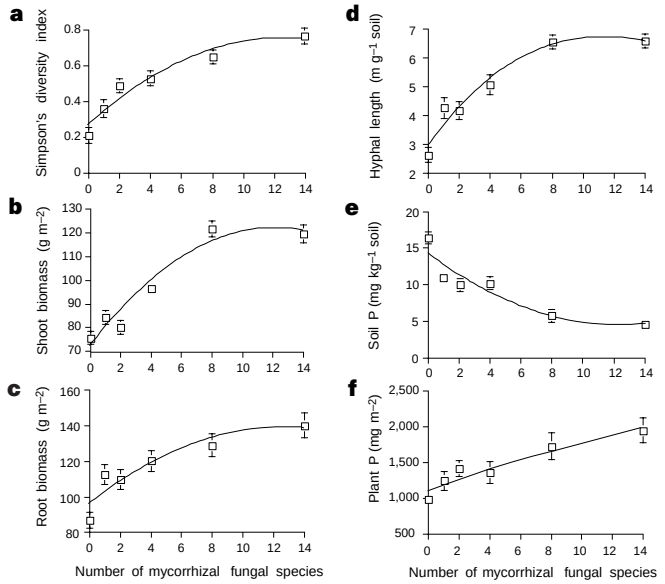

Figure 2 The effect of AMF-species richness on different parameters. Effects on: **a**, Simpson's diversity index (fitted curve is $y = 0.271 + 0.077x - 0.003x^2$; $r^2 = 0.63$; $P \leqslant 0.0001$); **b**, shoot biomass ($y = -0.334x^2 + 8.129x + 72.754$; $r^2 = 0.69$; $P \leqslant 0.0001$); **c**, root biomass ($y = -0.265x^2 + 6.772x + 96.141$; $r^2 = 0.55$; $P \leqslant 0.0001$); **d**, length of external mycorrhizal hyphae in soil ($y = 0.001x^3 - 0.046x^2 + 0.756x + 2.979$; $r^2 = 0.60$; $P \leqslant 0.0001$); **e**, soil phosphorus concentration ($y = 0.065x^2 - 1.593x + 14.252$; $r^2 = 0.67$; $P \leqslant 0.0001$); and **f**, total plant phosphorus content (linear relationship; $y = 61.537x + 1156.281$; $r^2 = 0.48$; $P \leqslant 0.001$), in macrocosms simulating North American old-field ecosystems (experiment 2). Squares represent means (± s.e.m.).

this possibility exists, but these results also show that different plant species benefit from different AMF taxa, which could explain the effects of increasing AMF-species richness. Furthermore, independent control experiments, in which inoculum densities of effective taxa were manipulated, never resulted in AMF hyphal densities as high as those seen as a result of species-rich AMF treatments in experiment 2. The observed differential effects of AMF species on the growth of plant species (as shown in experiment 1) and the potential resulting positive feedbacks between specific plant–fungal combinations[15] may, therefore, explain why an increase in the richness of AMF species (experiment 2) led to increased hyphal foraging capacity, improved resource use and increased productivity and plant biodiversity. Increasing plant biodiversity has been shown to lead to greater ecosystem productivity[3,4]. The significant positive correlation between a plant-biodiversity index and ecosystem productivity in experiment 2 (Pearson's $r = 0.70$, $P \leqslant 0.001$) shows that such a relationship exists. We have shown here that this relationship occurs as a result of altering the richness of AMF species.

Our results emphasize the importance of the mycorrhizal symbiosis as a determinant of plant biodiversity, ecosystem variability and productivity. The loss of AMF biodiversity, which occurs in agricultural systems[20,23] could, therefore, decrease both plant biodiversity and ecosystem productivity while increasing ecosystem instability. The loss of biodiversity in soils represents an understudied field of research which requires more attention. The present reduction in biodiversity on Earth and its potential threat to ecosystem stability and sustainability[1,4] can only be reversed or stopped if whole ecosystems, including ecosystem components other than plants, are protected and conserved. □

Methods

Experiment 1. We established 48 microcosms simulating European calcareous grassland under sterile greenhouse conditions in containers measuring $26.5 \times 17 \times 18\ cm^3$. These containers were filled with a 7.38-kg soil mixture of autoclaved quartz sand and autoclaved calcareous grassland soil (1:1 *v/v*). The microsoms were inoculated with 100-g soil inoculum of one AMF species (four single AMF-species treatments) or a mixture of the four AMF species, or were inoculated with an autoclaved (121 °C; 30 min) soil mixture of these four AMF species (the non-mycorrhizal control). The experiment was set up as a randomized block design in which each treatment was replicated eight times and each block was randomized every 2 weeks. In each microcosm, 70 seedlings of 11 calcareous grassland plant species were planted at random and put at fixed distances from each other. The number of seedlings of each plant species corresponded to natural abundances in a calcareous grassland in Switzerland. Microcosms received 380 ml filtered washing of soil inoculum (without AMF propagules) to correct for possible differences in microbial communities[24].

The four different AMF species, all belonging to the genus of *Glomus* (class: Zygomycete), were isolated from a calcareous grassland in Switzerland[21,22], and the calcareous grassland soil was obtained from a similar site. Detailed information about the four AMF taxa is published elsewhere[21,22] and further information on BEG AMF taxa can be obtained at http://wwwbio.ukc.ac.uk/cinetpubwwwroot/beg/begdatabase/amfreq%2Dreg.htm. All AMF isolates are both morphologically and genetically different from each other, but as three of the four taxa are undescribed we refer to them here as taxa and not species.

Microcosms were maintained in the greenhouse during two growing seasons and received a winter period from January to March 1997. Microcosms were watered three times a week and each microcosm was adjusted to an equal soil water content every two weeks by weighing. Above-ground plant parts were cut per plant individual in four regular harvests (mowing level 2.5 cm above soil surface) and were cut to the soil surface at the final harvest in December 1997. Total above-ground biomass of each plant species was determined, after drying at 70 °C, by adding the biomass of each of the five harvests.

Experiment 2. We established 70 macrocosms simulating North American old-field ecosystems under field conditions and inoculated them with 1 kg AMF inoculum containing 1, 2, 4, 8 or 14 species, which were randomly selected from a pool of 23 different AMF species. All AMF species were isolated from the Long-Term Mycorrhizae Research Site of the University of Guelph. The species were *Acaulospora denticulata*, *Acaulospora morrowiae*, *Acaulospora spinosa*, *Acaulospora* spp. 1 and 2 (undescribed), *Entrophospora colombiana*, *Gigaspora gigantea*, *Gigaspora margarita*, *Gigaspora rosea*, *Glomus claroideum*, *Glomus etunicatum*, *Glomus intraradices*, *Glomus macrocarpum*, *Glomus mosseae*, *Glomus* spp. 1–4 (undescribed), *Scutellospora calospora*, *Scutellospora dipurpurescens*, *Scutellospora heterogama* and *Scutellospora pellucida*. All mycorrhizal taxa were morphologically distinct from each other and are referred to here as species. The non-mycorrhizal control received 1 kg sterilized (γ-ray-irradiated) AMF inoculum. All macrocosms received 1 litre filtered washing of AMF inoculum to correct for possible differences in microbial communities[24]. We set up the experiment in a randomized design, each treatment being replicated ten times.

Each macrocosm was showered with a seed rain consisting of 100 seeds from each of the following 15 most abundant plant species of the research site: *Agrostis gigantea*, *Bromus inermis*, *Poa compressa*, *Achillea millefolium*, *Aster cordifolius*, *Aster novae-angliae*, *Chrysanthemum leucanthemum*, *Daucus carota*, *Euthamia graminifolia*, *Fragaria virginiana*, *Plantago lanceolota*, *Ranunculus acris*, *Rudbeckia hirta*, *Geum macrophyllum* and *Solidago canadensis*.

Each macrocosm, $1 \times 0.75 \times 0.25\ m^3$ contained a 90-kg mixture of γ-ray irradiated sand and soil (1:1 *v/v*). We fertilized macrocosms each month with a half-strength, low-phosphorus, Hoagland nutrient solution. After one growing season, plants were harvested and root and shoot biomass were determined after drying for 48 h at 60 °C. Plant biodiversity was assessed using Simpson's diversity index[25] on individual species shoot-biomass data. Plant biomass was assessed as total shoot and root biomass for the entire plant community. Shoot plant phosphorus concentrations were determined for each plant species and summed to give total shoot phosphorus content for each entire macrocosm. Root phosphorus concentration was measured from a mixed sample of roots, and total root phosphorus content was estimated for each entire macrocosm using the root biomass data. Soil phosphorus was assessed as bicarbonate-extractable soil phosphorus[26]. We measured AMF hyphal length on membrane filters[27].

In the non-mycorrhizal control, there was less than 3 m g^{-1} non-mycorrhizal hyphae; this represents a background count of non-mycorrhizal fungi in each treatment. In the non-mycorrhizal control treatments of experiments 1 and 2, plant roots were not colonized by AMF and no spores of AMF were found. For further information, readers may contact J.N.K.

Received 28 July; accepted 10 September 1998.

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Acknowledgements. This work was supported by the Swiss National Science Foundation and the Natural Sciences and Engineering Research Council of Canada. We thank P. Leadley, D. Read, P. Salzer, B. Schmid, J. Stocklin and D. Tilman for comments.

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Attention improves or impairs visual performance by enhancing spatial resolution

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Covert attention, the selective processing of visual information at a given location in the absence of eye movements, improves performance in several tasks, such as visual search and detection of luminance and vernier targets[1–6]. An important unsettled issue is whether this improvement is due to a reduction in noise (internal or external)[6–9], a change in decisional criteria[10,11], or signal enhancement[3,5,12]. Here we show that attention can affect performance by signal enhancement. For a texture segregation task in which performance is actually diminished when spatial resolution is too high, we observed that attention improved performance at peripheral locations where spatial resolution was too low, but impaired performance at central locations where spatial resolution was too high[4–12]. The counterintuitive impairment of performance that we found at the central retinal locations appears to have only one possible explanation: attention enhances spatial resolution.

We previously demonstrated that when a spatial cue directs covert attention to an upcoming target location, observers' performance improves for stimuli designed to measure spatial resolution (for example, the Landolt-square—a square with a small gap on one side)[5]. This 'peripheral cue' putatively draws covert attention to its location automatically[2,3,13]. Because the display characteristics ensured that neither a reduction in noise nor a change in decisional criteria could explain this attentional facilitation, this finding indicated that attention could enhance spatial resolution at the cue location[5]. Similarly, in visual search tasks in which observers'

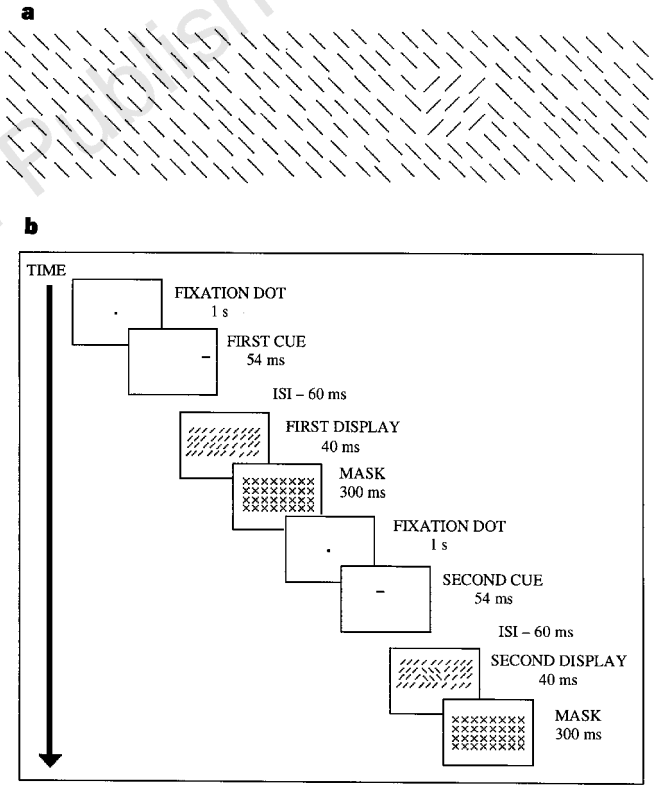

Figure 1 Texture segregation task. **a**, The display consisted of a 2 × 1.5 cm target-texture, composed of 3 × 3 lines (oriented at 45 or 135°), embedded in a background-texture composed of 287 lines (7 rows × 41 columns, subtending 5 × 28 cm) whose orientation was orthogonal to the target. The elements were jittered by 0.3 cm. From a viewing distance of 57 cm, the target subtended 2 × 1.5° of visual angle and the texture display subtended 5 × 14° of visual angle to each side of the centre of the display. The target appeared equally often in each interval (50% of the time) and was centred at any of 35 possible locations along the horizontal meridian in a random order. **b**, Each interval began with a fixation dot at the centre, followed by a brief cue. The cue was either 'peripheral' (a green horizontal bar of 0.3 × 0.6 cm appearing 0.3 cm above the target location) or neutral (two horizontal lines of 0.3 × 28 cm appearing above and below the display). After an interstimulus interval (ISI), the texture was displayed for an average of 40 ms. The ISI was set individually to keep overall performance level 75% correct; display duration ranged from 15 to 50 ms. A mask, with crosses as elements, followed the stimulus. Observers were asked to indicate the interval containing the target by pressing one of two keys. The order of the 100 practice trials, as well as that of the 288 experimental trials, was randomized.