TABLE 2 Factors influencing drought resistance

Variable	Partial correlation coefficient	P
Field A intercept	−0.39	<0.0001
Field B intercept	−0.30	<0.0001
Field C intercept	−0.20	0.003
ln (SR_{1989})	0.18	0.009
SR_{C3}	−0.18	0.012
Biomass of *Schizachyrium* (1989)	−0.16	0.027
SR_{C4}	−0.14	0.042

Partial correlations of each listed variable with deviation from pre-drought biomass, holding other listed variables constant. These seven variables were retained in multiple regression analysis of 1992 deviation from pre-drought biomass against the same candidate variables used in Table 1, but using 1989 values. Backwards elimination, with residual analysis, was used to retain only significant ($P < 0.05$) variables. The overall regression had $F = 14.0$, $n = 206$, $R^2 = 0.33$, $P < 0.0001$. SR_{C3} is the number of C3 species and SR_{C4} is the number of C4 species in plots in 1989. The significantly positive slope for ln (SR_{1989}) and the significantly negative intercepts for fields A, B and C indicate that species-poor plots in these fields have not yet attained pre-drought biomass, whereas more species-rich plots have. Field D, a native grassland, recovered most rapidly, followed by field C, then B, then A, in order of successional age.

natural logarithm of 1989 species richness. These indicate that species-poor plots were still further from their pre-drought biomass than were species-rich plots in each of the four post-drought years.

By 1992, species-rich plots had returned to pre-drought biomass, but the most depauperate plots still had significantly less biomass than their pre-drought average (Fig. 2). When potentially confounding variables were controlled for, there was a significant partial correlation between drought recovery and the natural logarithm of 1989 species richness ($r_{partial} = 0.184$, $P < 0.01$, $n = 207$). Moreover, when all redundant, nonsignificant variables were removed, species richness was retained, and its partial correlation was highly significant (Table 2). Thus, species-poor plots were both more greatly harmed by drought (Fig. 1 and Table 1) and took longer to return to pre-drought conditions (Fig. 2 and Table 2). The stand of native prairie was significantly more resilient than the three successional grasslands (Table 2).

Our results and earlier studies[5,12,14,15] support the diversity–stability hypothesis[5], and show that ecosystem functioning is sensitive to biodiversity. Our results do not support the species-redundancy hypothesis because we always found a significant effect of biodiversity on drought resistance and recovery even when we controlled statistically for the abundances of C3 (often drought sensitive) and C4 (often drought resistant) plant functional groups (Table 1).

Our results show that ecosystem resistance to drought is an increasing but nonlinear function of species richness. This is expected from the mechanism underlying the diversity–stability hypothesis. Functional diversity should be a saturating function of species richness because, in species-rich ecosystems, additional species are more likely to be similar to existing species[21]. Thus, the progressive loss of species should have progressively greater impacts on ecosystem stability.

In addition to drought, grassland ecosystems experience periodic invasions of insect or mammalian herbivores, unusually late or early frosts, unusually wet or cool years, hail, fire, and other perturbations. Because different species are likely to perform best for particular combinations of these disturbances, the long-term stability of primary production in these and other[12] grasslands should depend on their biodiversity. Although we do not know how the stability of other ecosystems depends on

biodiversity, these results lend further urgency to pleas for the conservation of biodiversity. □

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The role of partial occlusion in stereopsis

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MODELS of stereopsis typically assume that all the information about stereoscopic depth is contained in the disparity field, that is, the positional differences of image features that arise from surfaces visible to both eyes. But such models have difficulty in resolving image regions containing occlusions, because a portion of the occluded surface is visible to only one of the two eyes ('half-occlusions')[1]. Here I present displays revealing an unexpected relationship between interocular differences in image position and occluding contours. The partial occlusion of contours can give rise to both horizontal and vertical image differences that are not disparities. The results show that the visual system interprets these image differences as signalling the presence of occluding contours. Even when a single line segment serves as a binocular target, subjective contours form that can appear both oriented and in depth. These local subjective contours have a strong tendency to interact cooperatively and form global contours not present in the monocular images. These and other findings[2-4] show that stereoscopic processing actively decomposes vertical and horizontal image differences into disparities and half-occlusions. The two sources of information are complementary: while disparity provides relative depth information about surface features visible to both eyes, half-occlusions provide information to segment the visual world into coherent objects at object boundaries.

Previous theories of stereopsis have emphasized the relationship between interocular image displacements and binocular disparity. Indeed, the experience of stereoscopic depth was usually attributed to only the horizontal component of the disparity field[5,6]. Mayhew and Longuet-Higgins[7] challenged this view with a computational theory which demonstrated that the horizontal gradient of the vertical disparity field could be used to recover properties such as gaze angle and the absolute distance of surface features. Recent psychophysical experiments have revealed, however, that such gradients are either not used[8] or contribute less information than is theoretically obtainable[9].

One possible reason for the limited applicability of the Mayhew and Longuet-Higgens theory to human vision is that vertical image differences do not always represent vertical disparities. Indeed, occluding contours can generate both horizontal and vertical image displacements that are due to the presence of half-occlusions, not binocular disparities. This suggests a new way in which interocular differences in vertical position may influence stereoscopic depth, that is, by signalling the presence of an occluding contour. I present evidence here to support this idea. Figure 1a shows an example. When Fig. 1a is fused, observers report the appearance of an illusory window that is in front of and surrounds the line segments. This illusory window is also evident when the density of the lines is reduced (Fig. 1b, c). The illusions portrayed in Fig. 1 were created by lengthening the line segments in one of the two eyes. Hence, the subjective

contours (SCs) which formed are due solely to vertical image differences.

In theory, there are at least two ways that Fig. 1 could be perceived by the visual system. I will focus on one half of the stereopair in Fig. 1a to simplify the analysis of these patterns (Fig. 2a). One possibility is that the line terminators are matched, generating vertical disparities. Vertical disparities of this kind should cause the left and right halves of Fig. 1a to appear slanted in stereoscopic depth about a vertical axis of rotation, as has been shown previously for patterns such as random dot stereograms (known as the 'induced effect'; ref. 10; see
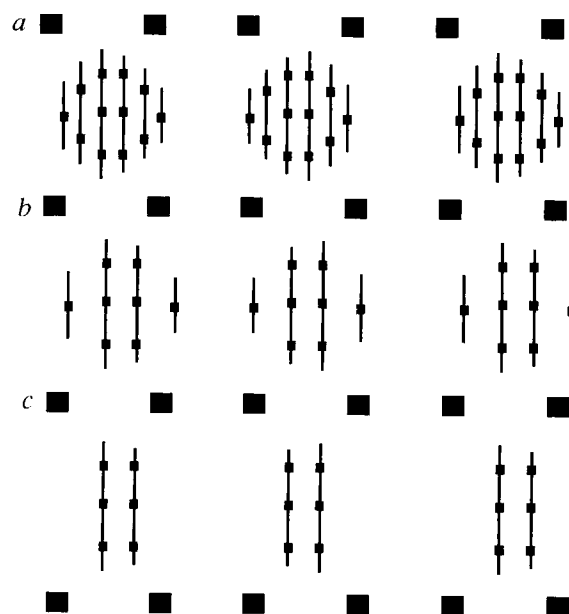

FIG. 1 Examples of the formation of subjective contours by interocular differences in vertical position. Cross-fusers should fuse the left two columns, divergers or viewing with a stereoscope should fuse the right two columns. In this and subsequent figures, the description of the SCs only holds for the pattern in which the line segments appear behind the small squares in the surround. In the central pattern of a, the rightmost three lines are slightly longer on both ends of the figure than the corresponding lines in the other eye's view. Similarly, the leftmost three lines of the central figure are smaller than the corresponding lines in the other eye's view. When fused, observers report the appearance of a compelling illusory 'window' that forms in front of the line segments as part of an apparent occluding surface. An occluding surface of this kind would produce the pattern of vertical image displacements depicted. The illusory window is apparent even when the density of the line segments is reduced to four (b) or two (c) line segments. The large squares in the surround and the small squares on the line segments in this and subsequent figures prevented eye and head movements from eliminating the vertical displacements of the line targets. They also served as reference disparities appropriate to the depth of the illusory window and line segments, respectively.
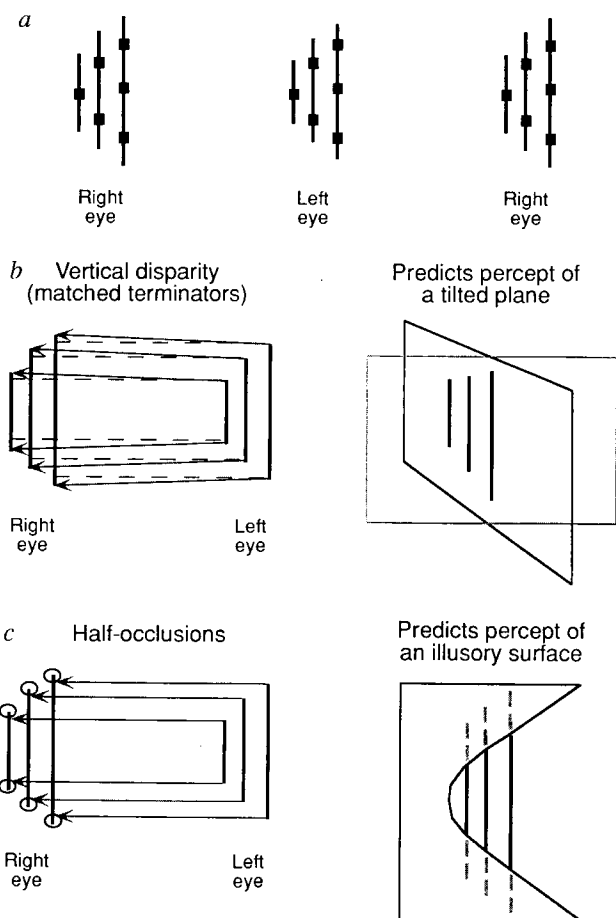

FIG. 2 Diagram of the possible interpretations of vertical image displacements for the left and right eye patterns depicted in a. In this stereopair, the line segments in the right eye's view are longer on the top and bottom than the left image. b, Diagram of the percept expected if the line terminators are matched, generating vertical disparities. In the left half of the figure, dashed lines served as references to depict the difference in height of the terminators in the two eyes; arrows indicate that the terminators are matched. The lines of the stereogram should appear to lie in a plane tilted in depth, as has been shown previously for patterns such as random-dot stereograms (known as the 'induced effect')[7]. This possible percept was shown to 33 observers, but none reported this experience. c, Diagram of the percept expected if the 'extra' line lengths in the right eye's view (terminators enclosed by circles) are treated as half-occlusions, that is, monocular features that arise from binocularly viewing scenes containing occluding surfaces. The grey region depicts the percept of an occluding surface that is in front of the line segments. No difference in the apparent luminance of these regions was reported and is presented only for schematic purposes. Note that this pattern of monocular features can only arise in natural viewing conditions if occluding surfaces are present. In these stereopairs, however, the occluding contours are not visible monocularly, but are created by interpreting the line terminators of the right eye as half-occlusions. This percept was observed by all subjects tested ($n = 33$; $P \ll 0.001$).

Stimuli
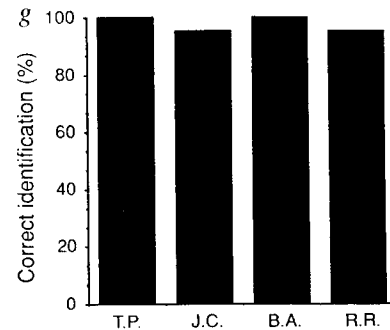
Percepts

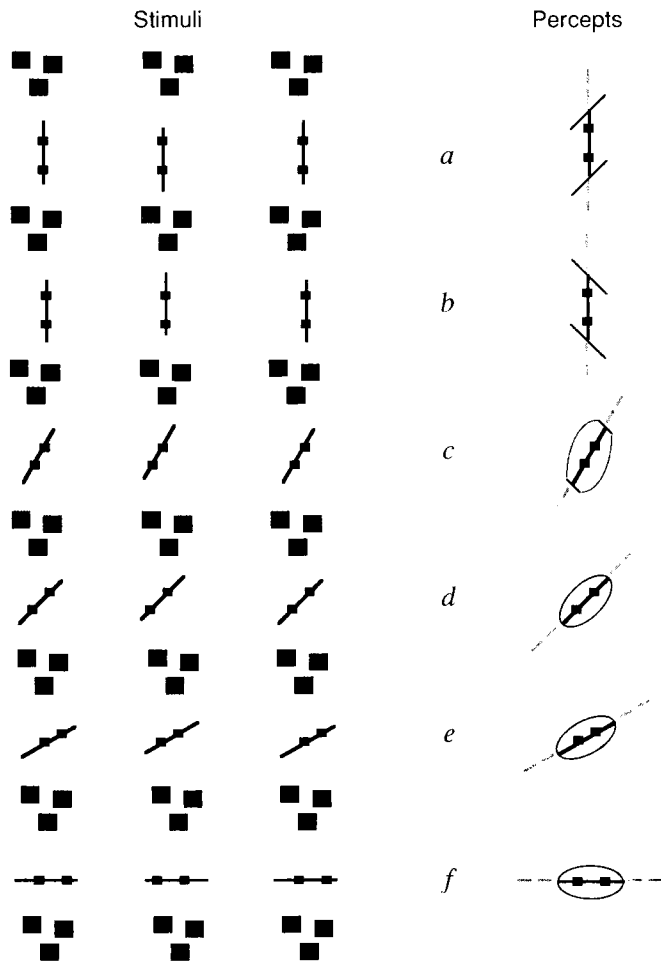*a*

b

c

d

e

f

g

FIG. 3 Patterns demonstrating the rich local structure generated by interpreting the vertical image difference of a single line terminator as a half-occlusion. Cross-fusers should fuse the left two columns, divergers the right two columns. As in the other figures, the description of the subjective contours only holds for line segments which appear behind the small squares in the surround. The far right column depicts the percepts that emerge. The SCs are seen in stereoscopic depth in front of the line segments. The length of the line segment was held constant in the two eyes, but a vertical interocular displacement was added to one of the line segments. The dots in the surround and on the line have only horizontal disparities. In *a*, a single vertical line segment can generate SCs that appear both oriented and in depth. Interchanging the two eye's views leads to a reversal in the perceived orientation of the SCs. To document perceptual sensitivity to this information, four observers were shown 30 stereopairs of patterns (*a* and *b*), presented in random order. Their task was to identify the sign of the SC's slope (that is, positive or negative). No feedback was given to prevent the association of an arbitrary cue to correct identification performance. As can be seen in *g*, observers (*x* axis) were essentially flawless in identifying the sign of the SC's orientation of patterns *a* and *b*. This task could only be performed accurately if the differences in vertical position of the contours were interpreted as half-occlusions. In patterns *c–f*, a diagram is presented of the percepts obtained for line segments that deviated from purely vertical. Observers report that the subjective contours not only appear to occlude the ends of the line segments, but also that they tend to 'complete' perceptually and to form illusory windows that surround the line segments. This result reveals strong co-operative interactions between the local SCs formed by interpreting the terminator of a contour as half-occluded. Note that *f* does not contain any vertical displacements, only horizontal ones, yet nonetheless vivid SCs form. This provides a conclusive control experiment that it is not the vertical displacement of the line segments *per se* that is responsible for the formation of the subjective contours; rather, it is the interpretation of the terminators as being half-occluded that generates these illusions.

FIG. 4 Stereopairs used to assess the nature of the interactions between the locally generated SCs revealed in the patterns in Fig. 3*a* and *b*. Again, cross-fusers should fuse the left two columns, divergers the right two columns. *a*, A stereopair demonstrating that the SCs can combine to form surfaces that are curved within a single, frontoparallel depth plane. *b*, Stereopair demonstrating that these SCs can form coherent contours across non-frontoparallel depth planes. Only the pattern which appears behind the dots in the surround have an occlusion interpretation, and only these figures are stable. The patterns that appear in front of the small squares generate unstable percepts at the terminators of the line segments.
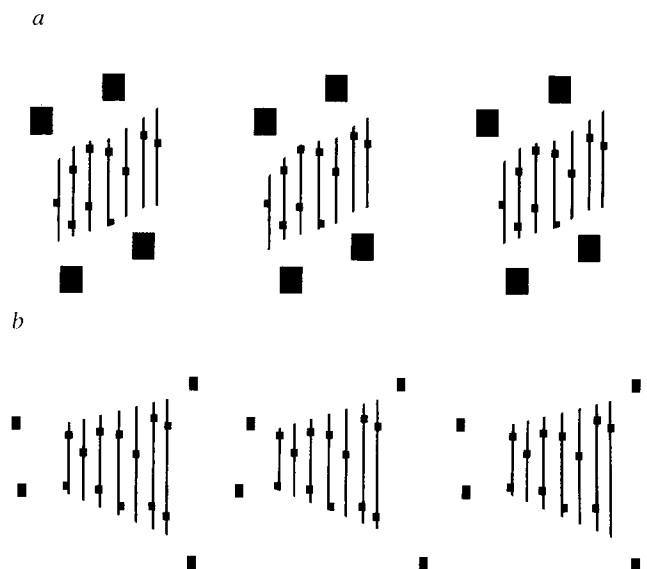
a

b

Fig. 2b). This percept was not experienced by any of the 33 observers tested. The second possibility is that portions of the line segments are left unmatched and treated as half-occlusions. An interpretation of this kind should lead to the formation of SCs[2,11] (Fig. 2c). Compelling SCs are indeed reported by all observers ($n = 33$; $P \ll 0.001$).

Even for a single contour, the SCs can exhibit both an orientation and a depth. Whereas SCs have been observed previously with half-occlusions that are completely hidden in one eye's view[2,11], an oriented depth signal was only perceived when a number of such half-occlusions were aligned. However, for partially occluded, vertically oriented contours, the sign of the occluding contour's orientation (that is, whether it is of positive or negative slope) can be derived by considering where the half-occlusions are relative to the portion of the line that is fused. For example, if the occluding contour has a positive slope (45°, say), it will produce half-occlusions in the right eye if it is above the vertical contour; but if the occluder is below the fused contour, it will produce half-occlusions in the left eye. Thus, it is the geometric relationship between the fused portion of the vertical contour and the half-occlusions which determines the sign of the SC's orientation. Experimental investigation reveals that observers can accurately identify the sign of the SC's orientation for a single vertical line (Fig. 3g). These findings provide conclusive evidence that the vertical displacements of the line segments are being interpreted as half-occlusions.

Another striking property of these SCs is their tendency to interact cooperatively and form global percepts of occluding surfaces. This can be observed for a line segment oriented between zero and ~60° (Fig. 3c–f). Observers report that SCs not only seem to occlude the ends of the line segments, but they also tend perceptually to close and form illusory oval apertures ($n = 33$; $P \ll 0.001$). This also has a real-world counterpart: an obliquely oriented contour viewed through an aperture would generate some half-occluded features at the ends of the line segments. However, this is not the only interpretation possible: this pattern of stimulation could also have arisen from two disconnected occluding surfaces rather than from a single, closed aperture. The striking quality of this demonstration is the robust tendency for the SCs perceptually to complete and form a single, global contour. Note that it is not the vertical interocular displacement per se that is responsible for these illusions, as Fig. 3f contains no vertical displacements. Rather, it is the interpretation of the terminators as half-occlusions that generates the SCs, which can occur for either horizontal or vertical image displacements.

Finally, the stereograms in Fig. 4 reveal that locally generated SCs can perceptually join neighbouring SCs to form curved contours within a single, frontoparallel depth plane (Fig. 4a), or form coherent contours across non-frontoparallel depth planes (Fig. 4b). Hence the interactions between these SCs are not limited to a single depth or co-linear contours. Note also that these SCs are only apparent when the image displacements are consistent with an occlusion configuration. Interchanging the images in the two eyes causes the terminators of the line segments to appear unstable; it does not invert the depth relationships (as would be expected if the terminators were matched and interpreted as disparities).

The relationship between image displacements and occlusion—especially vertical image displacements—has not been appreciated previously. The present findings demonstrate a new way in which vertical image differences can generate percepts of depth, even oriented depth percepts. Although it has long been believed that the primary goal of binocular processing is to generate a disparity map[5,6,12,13], the results described here demonstrate that binocular features are actively decomposed into disparities and half-occlusions. The need for this decomposition can be appreciated by considering the information contained in the two kinds of stereoscopic features. Disparity computations provide a rich representation of the surface regions visible to both eyes, but break down at the discontinuities of object boundaries that occlude other surfaces. The information contained in half-occlusions complements the information contained in disparity signals by providing a rich representation of the depth and orientation of object boundaries that arise at occluding contours. Both forms of information are needed to provide a clear representation of stereoscopic depth in environments replete with occluding contours, and both forms of information are used by the human visual system. □

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Neurotrophin-3 prevents the death of adult central noradrenergic neurons in vivo

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NEUROTROPHIN-3 (NT-3)[1–4] and neurotrophin-4/5 (NT-4)[5–7], together with nerve growth factor and brain-derived neurotrophic factor, are members of the neurotrophin family of proteins[8,9], which supports the survival of vertebrate neurons. However, no function in vivo has been described for NT-4 and limited information is available on the role of the other neurotrophins in the central nervous system in vivo. Nerve growth factor prevents the degeneration of lesioned septal cholinergic neurons in the adult brain[10–13], whereas brain-derived neurotrophic factor prevents the death of developing motor neurons[14–16] and a subpopulation of adult septal cholinergic neurons[17]. Finally, NT-3 partially prevents the death of facial motor neurons in newborn rats[16]. To assess the role of NT-3 and NT-4 in the adult brain in vivo, we implanted genetically modified fibroblasts that constitutively express high levels of NT-3 or NT-4. The results show that NT-3, but no other neurotrophin, prevents the degeneration of noradrenergic neurons of the locus coeruleus in a 6-hydroxydopamine lesion model that resembles the pattern of cell loss found in Alzheimer's disease[18,19]. These results imply that NT-3 may have therapeutic potential for preventing the death of noradrenergic neurons in the locus coeruleus.

Fischer rat 3T3 fibroblasts were co-transfected with a plasmid conferring resistance to the antibiotic G418 and the OVEC expression plasmid[17] containing a rat NT-3 complementary DNA[20] or the PCMX expression plasmid containing a rat NT-4 cDNA[7]. Clonal cell lines resistant to G418 were isolated and analysed. Southern blotting showed that cell lines designated F3A-NT3 and F3A-NT4 contained multiple copies of the NT-3 or NT-4 genes, respectively. Northern blotting (data not shown) and ribonuclease protection assays revealed that the cells expressed high levels of the corresponding NT-3 or NT-4 messenger RNA in culture (Fig. 1a, c). In addition, these cell lines continued to express high levels of the introduced neurotrophin gene at least one week after their implantation in the brain, as assessed by both RNase protection assay (Fig. 1a, c) and in