

Cytochem. **10**, 355 (1962).

14. Five 10- μ m sections (separated by at least 42 μ m) were selected for each cortical area analyzed. Neurons within layers II, III, and VI of the dorsolateral neocortex were counted at $\times 600$ by utilizing a grid containing four squares, which was mounted in the microscope eyepiece. Neurons were counted only if they contained a distinct nucleolus and only if more than half of the cell body was within the boundaries of the grid. Mean neuronal densities for each animal were used to compute the mean \pm SEM for lesion and control groups. One-way analysis of variance was used to determine significant differences between groups.
15. G. LoConte, L. Bartolini, F. Casamentia, I. Marconini-Pepeu, G. Pepeu, *Pharmacol. Biochem. Behav.* **17**, 933 (1982); C. Flicker, R. Dean, D. Watkins, S. Fisher, R. Bartus, *ibid.* **18**, 973 (1983); S. Dunnett *et al.*, *Neuroscience* **16**, 787 (1985); B. Knowlton *et al.*, *Brain Res.* **345**, 315 (1985); B. Dubois, W. Mayo, Y. Agid, M. LeMoal, H. Simon, *ibid.* **338**, 249 (1985); D. Hepler, D. Olton, G. Wenk, J. Coyle, *J. Neurosci.* **5**, 866 (1985).
16. P. N. Strong, E. M. Meyer, P. R. Mouton, G. W. Arendash, in preparation.
17. Our previous histological analysis of acetylcholinesterase-stained brain sections (6) revealed that the vast majority of large acetylcholinesterase-positive neurons within the nBM are destroyed by ibotenic acid infusions.
18. Cortical cholinergic activity remaining after nBM lesioning may be due to intrinsic cholinergic neurons in rodent, but not primate, cerebral cortex. To minimize the influence of these intrinsic cholinergic perikarya, we measured cholinergic markers in isolated nerve terminals.
19. It is not obvious why such an effect should be observed in nBM-lesioned animals, and, indeed, we have not observed this effect at any earlier time point (2 or 10 months) after nBM lesions nor has such an effect been reported in the literature. This effect may be spurious and not replicable. Alternatively, this nBM lesion-induced decrease in cortical norepinephrine (NE) levels may indicate that a relation exists between loss of nucleus basalis cholinergic neurons and a loss or dysfunction of NE neurons originating from the locus ceruleus, which provide noradrenergic innervation to the neocortex. Involvement of such NE neurons in AD is implicated from studies showing AD brains to have a marked loss of NE neurons within the locus ceruleus [L. L. Iversen *et al.*, *Neurosci. Lett.* **39**, 95 (1983)] and decreased NE concentrations in neocortex [R. Adolfsson *et al.*, *Br. J. Psychiatry* **135**, 216 (1979); D. Mann *et al.*, *J. Neurol. Neurosurg. Psychiatry* **45**, 113 (1982)].
20. S. R. Vincent *et al.*, *Nature (London)* **298**, 65 (1982); B. Chronwall, T. Chase, T. O'Donohue, *Neurosci. Lett.* **52**, 213 (1984); E. Jones and S. Stewart, *Res. Publ. Assoc. Res. Nerv. Ment. Dis.* **64**, 163 (1986).
21. R. Robbins, R. Sutton, S. Reichlin, *Brain Res.* **234**, 377 (1982).
22. T. Hesum, E. Majawe, L. Russett, H.-Y. T. Yang, *Soc. Neurosci. Abstr.* **12**, 997 (1986).
23. O. Ottersen, *J. Comp. Neurol.* **194**, 267 (1980); M. Mesulam, E. Mufson, B. Wainer, A. Levy, *Neuroscience* **11**, 1185 (1983).
24. D. Price *et al.*, *Ann. N.Y. Acad. Sci.* **396**, 145 (1982); A. Herzog and T. Kemper, *Arch. Neurol. (Chicago)* **37**, 625 (1980).
25. B. T. Hyman, G. W. Van Hoesen, A. R. Damasio, C. L. Barnes, *Science* **225**, 1168 (1984).
26. H. Wisniewski and R. Terry, *Prog. Neuropathol.* **2**, 1 (1973).
27. R. G. Struble, L. C. Cork, P. J. Whitehouse, D. L. Price, *Science* **216**, 413 (1982).
28. Since we have not seen any of these neuritic plaque-like structures in the brains of aged, 2-year-old rats (G. W. Arendash and J. Mazziotta, unpublished observations), they apparently do not occur spontaneously in the aging rat brain and would, therefore, appear to be the result of nBM lesioning.
29. W. Cowan, in *Contemporary Research Methods in Neuroanatomy*, W. J. H. Nauta and S. O. E. Ebesson, Eds. (Springer-Verlag, New York, 1970), pp. 217-236.
30. B. Hyman, G. Van Hoesen, A. Damasio, *Soc. Neurosci. Abstr.* **12**, 944 (1986).

31. A. Hirano and H. Zimmerman, *Arch. Neurol. (Chicago)* **7**, 227 (1962); M. Ball, *Acta Neuropathol.* **37**, 111 (1978).
32. C. A. Kitt *et al.*, *Science* **226**, 1443 (1984).
33. T. Arendt, V. Bigl, T. Tennstedt, A. Arendt, *Neuroscience* **14**, 1 (1985).
34. M. Karnovsky and J. Roots, *J. Histochem. Cytochem.* **12**, 219 (1964).

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Environmental Correlates of Food Chain Length

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In 113 community food webs from natural communities, the average and maximal lengths of food chains are independent of primary productivity, contrary to the hypothesis that longer food chains should arise when more energy is available at their base. Environmental variability alone also does not appear to constrain average or maximal chain length. Environments that are three dimensional or solid, however, such as a forest canopy or the water column of the open ocean, have distinctly longer food chains than environments that are two dimensional or flat, such as a grassland or lake bottom.

A COMMUNITY FOOD WEB (1) DESCRIBES the feeding relations in a community of organisms. A trophic species (2) (hereinafter species) in a web is a collection of organisms that feed on a common set of organisms and are fed on by a common set of organisms. Species x is linked to species y when energy flows from x to y , that is, when y feeds on x . A chain is an energy path or sequence of links that starts at a species that eats no other species in the web and ends at a species that is eaten by no other species in the web. The length of a chain is the number of links it comprises. The mean chain length of a web is the arithmetic average of the lengths of all chains in the web.

Two major hypotheses and one empirical generalization have been proposed to relate chain lengths to environmental conditions. The first hypothesis, known as the "energetic hypothesis" (3), proposes that chain length is limited by the inefficiency with which energy is transmitted by predation and by the minimal energy requirements of predators. Limited available energy may make it impossible to support enough individuals to maintain a population, may make it impossible for individuals to find enough prey to survive, or may constrain chain length through other mechanisms. In its simple form, this hypothesis predicts that chains should be longer in ecosystems with higher primary productivity. It has been tested experimentally (4) and rejected for

small artificial ecosystems, and it remains to be tested further experimentally. From a review of nine studies ranging from energetically impoverished to highly productive environments, Pimm (5) concluded that there was no evidence for food chains being longer in more productive habitats.

The second hypothesis, known as the dynamical stability hypothesis (6), is based on the finding in specific mathematical models of ecosystems that the longer the chains, the more severe the restrictions that must be imposed on the coefficients of the models for equilibrium to be feasible or stable. Further, in certain models, ecosystems with longer chains take longer to return to equilibrium once perturbed, so that webs with longer chains may be less likely to persist in nature. This hypothesis predicts that chains should be longer in ecosystems exempt from large perturbations. To our knowledge, there is no reported evidence for or against this hypothesis.

The empirical generalization (7), based on 34 webs, proposes that chains tend to be longer in three-dimensional than in two-dimensional environments. An environment is classified as having dimension 2 if it is essentially flat, like a grassland, the tundra, a sea or lake bottom, a stream bed, or the rocky intertidal zone. An environment is classified as having dimension 3 if it is solid, like the pelagic water column or a forest canopy. Webs from habitats integrating both flat and solid environments are considered as having "mixed" dimension.

To evaluate the relative influence on chain length of the primary productivity, the variability, and the dimensionality of the environment, we studied a collection of 113

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webs, culled from 89 published and 2 unpublished studies, to cover as wide a diversity of natural environments as possible. Most of the world biomes are represented. There are 55 continental (23 terrestrial and 32 aquatic), 45 coastal, and 13 oceanic webs, ranging from arctic to antarctic regions.

Only webs partially defined, presented too sketchily, or based on information explicitly drawn from different locations were excluded from this collection. The webs were not screened by rejection of outliers or by any other statistical procedure based on the data. Only obvious biological errors were amended in editing the data. Although all webs were treated consistently in this collection, the practices of field ecologists in observing and reporting webs are not standardized. As the apparent characteristics of an individual web may reflect the idiosyncrasies of its observer, it is appropriate with these data to attend to broad trends and major differences among distributions.

The 113 webs studied are listed in Table 1 together with their sources and the following characteristics: mean chain length, maximal chain length, number of species, number of links, productivity, variability, dimensionality, and geographic origin. The details of 40 of these webs are fully documented (1, 8); the frequency distributions of chain length of all 113 webs have been reported (9). This large collection allows comparisons to be made that are more sensitive than before to small differences in mean chain length.

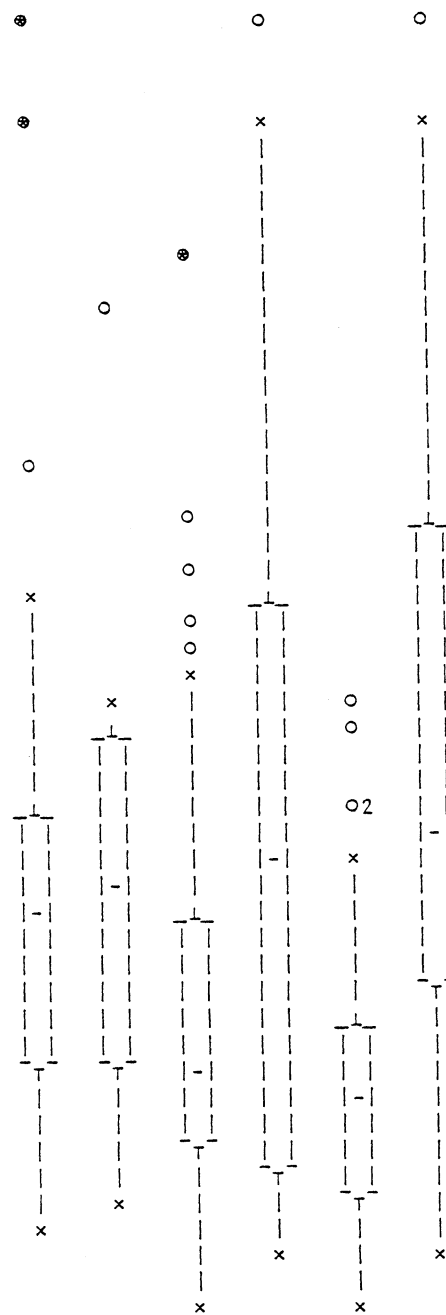
The productivity of a web is classified as low if the net primary productivity of its ecosystem falls below 100 g of carbon per square meter per year and high if it exceeds 1000 g of carbon per square meter per year. Of 113 webs, 22 were classified as having

low productivity, 10 as having high productivity, and 6 as having intermediate productivity. The remaining 75 webs were unclassified for want of information.

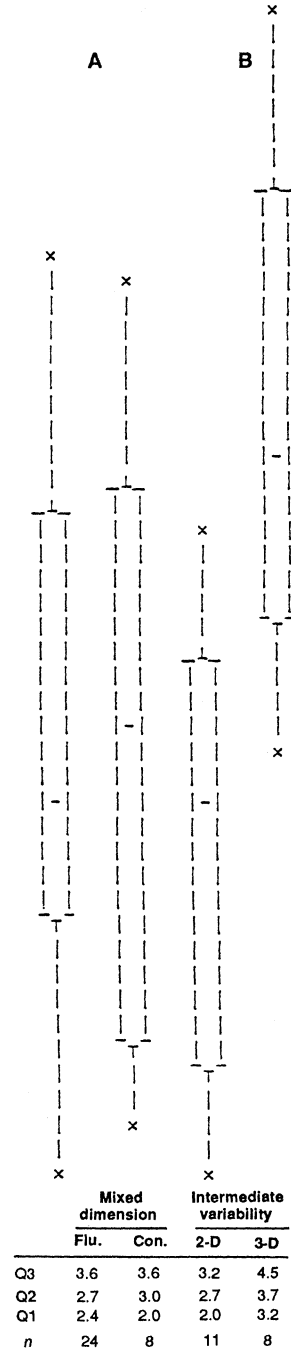
The variability of a web's habitat is classified as fluctuating or constant. The environment is fluctuating if the original report indicates temporal variations of substantial magnitude in temperature, salinity, water availability, or any other major physical pa-

rameter. The magnitude, not the predictability, of the variations is the criterion of classification. Of 113 webs, 64 were classified as fluctuating and 17 as constant. The remaining 32, previously (9) unclassified, are considered here as intermediate.

Of 113 webs, 40 were classified as having dimension 2 and 28 as having dimension 3. Forty-five webs previously (9) recorded as having neither dimension 2 nor dimension 3



	Productivity		Variability		Dimension	
	Low	High	Flu.	Con.	2	3
Q3	3.3	3.6	3.0	4.0	2.6	4.3
Q2	3.0	3.0	2.5	3.2	2.4	3.2
Q1	2.5	2.4	2.2	2.1	2.0	2.7
n	22	10	64	17	40	28



	Mixed dimension		Intermediate variability	
	Flu.	Con.	2-D	3-D
Q3	3.6	3.6	3.2	4.5
Q2	2.7	3.0	2.7	3.7
Q1	2.4	2.0	2.0	3.2
n	24	8	11	8

Fig. 2. Box plots of the frequency distributions of mean (within-web) chain lengths (A) in webs of mixed dimension, comparing fluctuating (Flu.) and constant (Con.) environments and (B) in webs of intermediate variability, comparing two- and three-dimensional environments. Symbols and other abbreviations are as in Fig. 1.

are here considered as having mixed dimension.

Some subjective judgments are involved in classifying webs as fluctuating or constant and as two-dimensional or three-dimensional. For the first 40 webs in the series (1, 8), the facts supporting these judgments are already documented.

All calculations were performed for both mean and maximal chain lengths. Maximal chain lengths varied in parallel with mean chain lengths throughout. We present the mean (within-web) chain lengths descriptively using box plots (10, 11). We attempt no formal statistical tests of differences between distributions because it is doubtful that the webs in our collection form a random sample from a well-defined universe of webs (9).

Figure 1 shows that the distributions of mean chain lengths are similar, with virtually identical medians, in webs differing markedly in productivity. Contrary to the energetic hypothesis, high-energy systems do not support longer chains, on average or maximally, than energetically impoverished environments. The possibility remains that energy influences chain length but that highly productive systems attract a greater fraction of energetically less efficient consumers, which prevent the assembly of longer food chains. Lacking detailed data on the energetic efficiency of the web species, we cannot exclude this possibility (12).

The distributions of mean chain lengths are relatively distinct in fluctuating compared to constant webs and quite distinct in webs having dimension 2 compared to those having dimension 3. The upper quartile of mean (within-web) chain length for the 40 webs of dimension 2 is 2.6 links, which falls below the lower quartile (2.7 links) of mean chain length for the 28 webs of dimension 3 (13).

It would be hasty to conclude that variability and dimensionality independently influence chain length. Of the two-dimensional webs, 27 are fluctuating and 2 are constant; of the three-dimensional webs, 13 are fluctuating and 7 are constant. Thus the proportion of constant webs is more than five times as high among three-dimensional webs as among two-dimensional webs. No such risk of confounding affects the interpretation of the effect of productivity in Fig. 1, since webs from environments with low or high productivity include comparable fractions of fluctuating and constant, and two-dimensional and three-dimensional, habitats (13).

To assess the relative influence of environmental dimension and variability on chain lengths, we compared the distributions among webs of mean (within-web) chain

lengths in fluctuating and constant webs having comparable, mixed dimension (Fig. 2A) and in two- and three-dimensional webs of comparable variability in constant, fluctuating, or intermediate habitats (the last comparison being shown in Fig. 2B).

If environmental variability alone markedly affects the length of chains, then the distributions in Fig. 2A should be distinct. That is not the case: given a mixed dimension, constant environments do not support markedly longer chains than fluctuating environments, contrary to the dynamic stability hypothesis.

If environmental dimension alone markedly affects chain length, then the distributions for webs with intermediate variability in Fig. 2B should be distinct. That is clearly the case. Further, in fluctuating habitats, the 27 webs with dimension 2 have a median 2.3 mean chain length, less than the median

2.8 mean chain length of the 13 webs with dimension 3. In constant habitats, the two webs with dimension 2 have a median 2.3 mean chain length, less than the median 4.0 mean chain length of the seven webs with dimension 3. Although there are too few webs in constant two- or three-dimensional habitats to justify any firm conclusion, the differences are consistent in the three comparisons: controlling for variability, webs in two-dimensional habitats have shorter mean chain lengths than those in three-dimensional habitats.

We conclude from our data that the dimensionality of the environment influences mean or maximal chain length more than environmental variability. Dimensionality is a major determinant of chain length in natural communities. Why this is so remains to be explained, although it is evident that environmental dimension may affect the

Table 1. Characteristics and sources of 113 webs. Serial numbers are the same as in Briand (7, 8) and in all previous joint publications of Briand and Cohen (2, 9). Productivity: 0, unclassified (unknown or intermediate); 1, low; 2, high. Variability: 0, intermediate; 1, fluctuating; 2, constant. Dimension: 0,

Web number	Mean chain length	Max. chain length	Number of trophic species	Number of links	Prod.	Var.	Dim.	Habitat	Ref.
1	3.13	4	8	14	0	0	0	Cochin Backwater, India	14
2	2.71	3	14	22	0	1	0	Knysna Estuary, South Africa	15
3	2.30	3	24	34	0	1	2	Salt marsh, Long Island, USA	16
4	2.74	4	13	26	0	1	0	Salt marsh, California	17
5	2.00	2	6	5	2	0	0	Salt marsh, Georgia	18
6	3.82	6	25	43	0	1	0	Tidal flat, California	19
7	2.79	4	18	30	0	0	0	Narragansett Bay, Rhode Island	20
8	2.44	4	15	25	2	1	0	Salt marsh, Rhode Island	21
9	2.86	3	9	13	0	0	0	Lough Ine Rapids, Ireland	22
10	2.00	2	3	2	0	1	2	Exposed rocky shore, New England, USA	23
11	2.00	2	5	4	0	1	2	Protected rocky shore, New England, USA	23
12	2.25	3	9	13	0	1	2	Exposed rocky shore, Washington	23
13	2.50	3	9	14	0	1	2	Protected rocky shore, Washington	23
14	2.40	3	8	10	0	0	0	Mangrove swamp 1, Hawaii	24
15	2.33	3	7	7	0	1	0	Mangrove swamp 3, Hawaii	24
16	2.14	3	14	20	2	1	0	Pamlico Estuary, North Carolina	25
17	3.56	5	14	23	0	0	3	Coral reefs, Marshall Islands	26
18	2.00	4	23	35	0	0	0	Kapingamarangi Atoll, Polynesia	27
19	3.00	4	17	32	1	1	3	Moosehead Lake, Maine	28
20	3.26	5	19	30	1	0	3	Antarctic Pack Ice Zone	29
21	4.61	7	9	20	0	0	3	Ross Sea	30
22	3.69	7	28	58	0	1	0	Bear Island, Spitsbergen	31
23	2.40	4	15	27	0	1	2	Prairie, Manitoba	32
24	2.70	4	12	18	0	1	3	Willow forest, Manitoba	32
25	2.16	4	24	37	0	1	3	Aspen communities, Manitoba	32
26	2.93	6	32	56	0	1	0	Aspen forest, Manitoba	32
27	2.89	4	22	39	2	1	3	Wythan Wood, England	33
28	1.96	3	32	35	0	1	0	Salt meadow, New Zealand	34
29	3.14	5	16	22	1	0	3	Arctic Seas	35
30	5.02	7	14	32	1	0	3	Antarctic Seas	36
31	3.90	6	14	51	0	0	3	Epiplankton communities, Black Sea	37
32	3.86	6	14	52	0	2	3	Bathypelagic communities, Black Sea	37
33	1.93	4	29	48	0	2	0	Crocodile Creek, Malawi	38
34	2.56	4	12	27	0	2	2	River Clydach, Wales	39
35	2.72	4	13	36	0	0	2	Morgan's Creek, Kentucky	40
36	2.07	4	19	35	0	0	0	Mangrove swamp 6, Hawaii	24
37	2.75	4	24	46	0	2	0	Marine sublittoral, southern California	41
38	2.13	3	31	95	0	2	0	Lake Nyasa, rocky shore, Malawi	38
39	1.80	3	33	70	0	2	0	Lake Nyasa, sandy shore, Malawi	38
40	1.88	3	11	15	0	2	3	Rain forest, Malaysia	42
41	5.92	8	18	49	1	2	3	Tropical seas, epipelagic zone	43
42	4.95	8	15	36	2	2	3	Upwelling areas, Pacific Ocean	44
43	3.13	5	20	38	0	2	3	Kelp bed community, South California	45
44	3.63	5	12	29	2	2	0	Marine coastal lagoons, Guerrero, Mexico	46
45	2.14	3	11	20	0	2	2	Cone Spring, Iowa	47
46	4.43	8	19	68	1	0	3	Lake Texoma, Texas	48
47	4.22	5	27	50	0	2	0	Swamps, south Florida	49
48	3.53	5	13	20	0	1	0	Nearshore marine 1, Aleutian Islands	50
49	2.56	4	12	20	0	1	0	Nearshore marine 2, Aleutian Islands	50
50	2.44	3	14	23	0	1	2	Sand beach, California	51
51	3.28	5	25	46	0	0	0	Shallow sublittoral, Cape Ann, Massachusetts	52
52	2.08	3	20	32	0	1	2	Rocky shore, Torch Bay, Alaska	53
53	1.95	2	22	31	0	1	2	Rocky shore, Cape Flattery, Washington	53
54	2.58	4	14	20	0	0	0	Western rocky shore, Barbados	54
55	2.46	3	12	18	2	1	2	Mudflat, Ythan Estuary, Scotland	55
56	2.22	3	10	14	0	1	2	Mussel bed Ythan Estuary, Scotland	55
57	3.29	5	9	19	2	0	0	Brackish lagoons, Guerrero, Mexico	46

probability per unit time of an encounter between predator and prey.

REFERENCES AND NOTES

1. J. E. Cohen, *Food Webs and Niche Space* (Monographs in Population Biology, no. 11, Princeton Univ. Press, Princeton, NJ, 1978).
2. F. Briand and J. E. Cohen, *Nature (London)* **307**, 264 (1984).
3. G. E. Hutchinson, *Am. Nat.* **93**, 145 (1959).
4. Special issue on Trophic Exploitation, S. L. Pimm and R. L. Kitching, *Oikos*, in press.
5. S. L. Pimm, *Food Webs* (Population and Community Biology Series, Chapman and Hall, London, 1982).
6. _____ and J. H. Lawton, *Nature (London)* **268**, 329 (1977).
7. F. Briand, in *Current Trends in Food Web Theory*, D. L. DeAngelis, W. M. Post, G. Sugihara, Eds. (Oak Ridge National Laboratory Report 5983, Oak Ridge, TN, 1983), pp. 37–39.
8. _____, *Ecology* **64**, 253 (1983).
9. J. E. Cohen, F. Briand, C. M. Newman, *Proc. R. Soc. London Ser. B* **228**, 317 (1986).
10. J. W. Tukey, *Exploratory Data Analysis* (Addison-Wesley, Reading, MA, 1977; reprinted by University Microfilms International, Ann Arbor, MI).

11. D. R. McNeil, *Interactive Data Analysis, A Practical Primer* (Probability and Mathematical Statistics Series, Wiley, New York, 1977).
12. P. Yodzis, in *Current Trends in Food Web Theory*, D. L. DeAngelis, W. M. Post, G. Sugihara, Eds. (Oak Ridge National Laboratory Report 5983, Oak Ridge, TN, 1983), pp. 41–44.
13. With a sufficiently large collection of fully described webs, it would be possible to cross-classify each web by its productivity, variability, and dimension and thereby to study the dependence of chain length on all three variables simultaneously. When the 113 webs are cross-classified by the variability and dimension of the environment only (and not by productivity, which is unknown for many webs), there are only two webs in constant environments of dimension 2. There are 27 webs in fluctuating environments of dimension 2, and this is the largest number in any cell of the cross-classification. Not enough webs are available to support further cross-classification.
14. S. Z. Qazim, in *Marine Food Chains: Proceedings of a Symposium Held at the University of Aarhus, Denmark, from 23rd to 26th July 1968*, J. H. Steele, Ed. (Oliver and Boyd, Edinburgh, 1970), pp. 46–51.
15. J. H. Day, in *Estuaries*, G. H. Lauff, Ed. (AAAS Publication 83, Washington, DC, 1967), pp. 397–407.

16. G. M. Woodwell, *Sci. Am.* **216**, 24 (March 1967).
17. R. F. Johnston, *Wilson Bull.* **68**, 91 (1956).
18. J. M. Teal, *Ecology* **43**, 614 (1962).
19. G. E. MacGinitie, *Am. Midl. Nat.* **16**, 629 (1935).
20. J. N. Kremer and S. W. Nixon, *A Coastal Marine Ecosystem: Simulation and Analysis*, vol. 24 of *Ecological Studies* (Springer-Verlag, Berlin, 1978).
21. S. W. Nixon and C. A. Oviatt, *Ecol. Monogr.* **43**, 131 (1973).
22. J. A. Kitching and F. J. Ebling, *Adv. Ecol. Res.* **4**, 197 (1967).
23. B. A. Menge and J. P. Sutherland, *Am. Nat.* **110**, 351 (1976).
24. G. E. Walsh, in *Estuaries*, G. H. Lauff, Ed. (AAAS Publication 83, Washington, DC, 1967), pp. 420–431.
25. B. J. Copeland, K. R. Tenore, D. B. Horton, in *Coastal Ecological Systems of the United States*, H. T. Odum, B. J. Copeland, E. A. McMahan, Eds. (Conservation Foundation, Washington, DC, 1974), vol. 2, pp. 315–357.
26. R. Hiatt and D. W. Strasburg, *Ecol. Monogr.* **30**, 65 (1960).
27. W. A. Niering, *ibid.* **33**, 131 (1963).
28. J. L. Brooks and E. S. Deevey, in *Limnology in North America*, D. G. Frey, Ed. (Univ. of Wisconsin Press, Madison, 1963), pp. 117–162.
29. G. A. Knox, in *Antarctic Ecology*, M. W. Holdgate, Ed. (Academic Press, New York, 1970), vol. 1, pp. 69–96.
30. B. C. Patten and J. T. Finn, in *Theoretical Systems Ecology: Advances and Case Studies*, E. Halfon, Ed. (Academic Press, New York, 1979), pp. 184–212.
31. V. S. Summerhayes and C. S. Elton, *J. Ecol.* **11**, 214 (1923).
32. R. D. Bird, *Ecology* **11**, 356 (1930).
33. G. C. Varley, in *Animal Populations in Relation to Their Food Resources*, A. Watson, Ed. (Blackwell Scientific, Oxford, England, 1970), pp. 389–401.
34. K. Paviour-Smith, *Trans. R. Soc. N.Z.* **83**, 525 (1956).
35. M. J. Dunbar, *Arctic* **7**, 213 (1954).
36. N. A. Mackintosh, in *Biologie Antarctique*, R. Carrick, M. Holdgate, J. Prevost, Eds. (Hermann, Paris, 1964), pp. 3–38.
37. T. S. Petipa, E. V. Pavlova, G. N. Mironov, in *Marine Food Chains*, J. H. Steele, Ed. (Oliver and Boyd, Edinburgh, 1970), pp. 142–167.
38. G. Fryer, *Proc. Zool. Soc. London* **132**, 153 (1959).
39. J. R. Jones, *J. Anim. Ecol.* **18**, 142 (1949).
40. G. W. Minshall, *Ecology* **48**, 139 (1967).
41. T. A. Clarke, A. O. Flechsig, R. W. Grigg, *Science* **157**, 1381 (1967).
42. J. L. Harrison, *J. Anim. Ecol.* **31**, 53 (1962).
43. N. V. Parin, *Ichthyofauna of the Epipelagic Zone* (Israel Program for Scientific Translations, Jerusalem, 1970).
44. M. E. Vinogradov and E. A. Shushkina, *Mar. Biol.* **48**, 357 (1978).
45. R. J. Rosenthal, W. D. Clarke, P. K. Dayton, *Fish. Bull. (Dublin)* **72**, 670 (1974).
46. A. Yanez-Arancibia, *Cent. Cienc. del Mar Univ. Nal. Auton. Mex. Publ. Espec.* **2**, 1 (1978).
47. L. J. Tilly, *Ecol. Monogr.* **38**, 169 (1968).
48. B. C. Patten et al., in *Systems Analysis and Simulation in Ecology*, B. C. Patten, Ed. (Academic Press, New York, 1975), vol. 3, pp. 205–421.
49. L. D. Harris and G. B. Bowman, in *Grasslands, Systems Analysis and Man*, A. I. Breyer and G. M. Van Dyne, Eds. (International Biological Programme Series, no. 19, Cambridge Univ. Press, Cambridge, England, 1980), pp. 591–607.
50. C. A. Simenstad, J. A. Estes, K. W. Kenyon, *Science* **200**, 403 (1978).
51. J. W. Nybakken, *Marine Biology: An Ecological Approach* (Harper and Row, New York, 1982).
52. R. W. Dexter, *Ecol. Monogr.* **17**, 263 (1947).
53. R. T. Paine, *J. Anim. Ecol.* **49**, 667 (1980).
54. F. Briand, unpublished observations.
55. H. Milne and G. M. Dunnet, in *The Estuarine Environment*, R. S. K. Barnes and J. Green, Eds. (Elsevier, New York, 1972) pp. 86–106.
56. N. N. Smirnov, *Hydrobiologia* **17**, 175 (1961).
57. A. C. Twomey, *Ecol. Monogr.* **15**, 175 (1945).
58. D. I. Rasmussen, *ibid.* **11**, 228 (1941).
59. V. S. Summerhayes and C. S. Elton, *J. Ecol.* **16**, 193 (1928).
60. J. R. Jones, *J. Anim. Ecol.* **19**, 159 (1950).

mixed; 2, two dimensional; 3, three dimensional. The source indicates the reference containing the original information (graphic or otherwise) about the food web.

Web number	Mean chain length	Max. chain length	Number of trophic species	Number of links	Prod.	Var.	Dim.	Habitat	Ref.
58	4.28	7	17	21	0	1	0	Spnagnum bog, Russia, USSR	56
59	2.37	4	29	61	0	1	3	Trelease Woods, Illinois	57
60	2.36	3	33	69	0	1	3	Montane forest, Arizona	58
61	2.00	3	8	10	1	1	2	Barren regions, Spitsbergen	59
62	3.00	4	11	12	1	1	2	Reindeer pasture, Spitsbergen	59
63	3.16	4	18	75	0	0	2	River Rheidol, Wales	60
64	1.67	2	19	28	0	0	2	Linesville Creek, Pennsylvania	61
65	1.85	2	13	25	0	0	2	Yoshino River Rapids, Japan	62
66	2.93	4	10	18	0	0	2	River Thames, England	63
67	3.94	6	21	62	0	0	0	Mudflats, Mississippi River, Iowa	64
68	2.63	4	22	32	0	1	3	Loch Leven, Scotland	65
69	3.62	6	29	73	0	1	0	Tagus Estuary, Portugal	66
70	2.49	3	14	28	0	1	0	Crystal River Estuary, Florida	67
71	5.15	7	16	32	0	1	3	Lake Rybinsk, Russia, USSR	68
72	3.95	5	17	32	0	1	3	Heney Lake, pelagic zone, Quebec	69
73	2.38	3	10	15	0	1	3	Hafner Lake, Austria	70
74	2.38	4	21	36	0	1	2	Sand beach, South Africa	71
75	2.75	4	9	14	0	1	3	Vorderer Finstertaler Lake, Austria	72
76	2.67	4	14	17	1	1	0	Neusiedler Lake, Austria	73
77	3.63	5	13	24	0	2	0	Lake Abaya, Ethiopia	74
78	3.15	5	16	27	2	2	0	Lake George, Uganda	75
79	3.41	5	21	29	0	1	0	Lake Pääjärvi, offshore, Finland	76
80	3.35	5	27	70	0	1	0	Lake Pääjärvi, littoral zone, Finland	76
81	2.73	4	12	19	1	0	0	Sendai Bay, mesopelagic zone, Japan	77
82	3.71	5	10	14	0	1	0	Permanent freshwater rockpool, France	78
83	2.45	4	25	67	1	1	0	Lake Pyhäjärvi, littoral zone, Finland	79
84	3.61	5	12	23	0	1	0	Temporary pond, Michigan	80
85	3.61	5	27	49	2	1	0	Tasek Bera Swamp, Malaysia	81
86	4.09	6	16	37	0	1	3	Suruga Bay, epipelagic zone, Japan	82
87	2.91	4	11	17	1	0	0	Ice edge community, High Arctic, Canada	83
88	1.95	2	16	42	0	0	2	Lestijoki River Rapids, Finland	84
89	2.89	4	18	32	0	0	3	River Cam, England	85
90	1.84	2	22	39	0	1	2	Old field, New Jersey	86
91	3.00	4	10	13	0	1	3	Shigayama coniferous forest, Japan	87
92	2.00	3	18	18	1	0	2	High Himalayas community, Tibet	88
93	2.12	3	26	70	1	1	2	Alpine tundra, Montana	89
94	3.35	5	12	19	1	1	2	Wet coastal tundra, Barrow, Alaska	90
95	2.50	4	10	12	1	1	2	Tundra, Prudhoe, Alaska	91
96	1.92	2	9	16	1	1	2	Tundra, Yamal Peninsula, Siberia	92
97	2.00	3	11	17	1	1	2	Tundra, South Yamal, Siberia	93
98	3.54	5	17	39	1	0	2	Sand dunes, Namib Desert, Namibia	94
99	2.51	4	48	138	1	0	2	Sonora Desert, Arizona	95
100	3.34	6	22	59	1	0	2	Rajasthan Desert, India	96
101	1.67	2	6	5	0	1	0	Temporary freshwater rockpool, France	78
102	3.97	7	9	27	1	2	3	Plankton, Oligotrophic Tropical Pacific	97
103	5.59	10	23	133	1	2	3	Tropical plankton community, Pacific	98
104	3.16	5	27	62	0	0	2	Rocky shore, Bay of Panama	99
105	3.67	5	10	22	0	1	2	Rocky shore, Gulf of Maine, USA	100
106	2.41	5	35	73	0	1	2	Rocky shore, Monterey Bay, California	101
107	2.50	3	10	14	0	1	2	Bay pilings community, New Jersey	102
108	2.27	3	14	20	0	1	2	Rocky shore, Cabrillo Point, California	103
109	2.88	4	21	57	0	1	2	Rocky shore, central Chile	104
110	2.13	3	13	23	0	1	2	Rocky shore, Cape Ann, Massachusetts	52
111	2.44	3	19	36	0	1	2	Mudflat, Cape Ann, Massachusetts	52
112	1.83	3	14	17	0	1	0	Low salt marsh, Cape Ann, Massachusetts	52
113	2.11	3	11	12	0	1	0	High salt marsh, Cape Ann, Massachusetts	52

61. K. W. Cummins, W. P. Coffman, P. A. Roff, *Verh. Int. Ver. Theor. Angew. Limnol.* **16**, 627 (1966).
62. M. Tsuda, in *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska, Eds. (Polish Scientific, Warsaw, 1972), pp. 829–841.
63. K. H. Mann *et al.*, *ibid.*, pp. 579–596.
64. C. A. Carlson, *Ecology* **49**, 162 (1968).
65. N. C. Morgan and D. S. McLusky, *Proc. R. Soc. Edinburgh* **74**, 407 (1972).
66. L. Saldanha, *Estudio Ambiental do Estuario do Tejo* (CNA/Tejo, Lisbon, 1980).
67. W. M. Kemp *et al.*, in *Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories*, C. A. Hall and J. W. Day, Jr., Eds. (Wiley, New York, 1977), pp. 507–543.
68. Y. I. Sorokin, in *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska, Eds. (Polish Scientific, Warsaw, 1972), pp. 493–503.
69. A. Baril, thesis, University of Ottawa, Canada (1983).
70. F. Schiemer *et al.*, *Sitzungsber. Akad. Wiss. Wien Math. Naturwiss. Kl. Abt. I* **191**, 209 (1982).
71. A. C. Brown, *S. Afr. J. Sci.* **60**, 35 (1964).
72. R. Pechlaner *et al.*, *Verh. Dtsch. Zool. Ges.* **65**, 47 (1972).
73. F. Schiemer, in *Neusiedlersee: The Limnology of a Shallow Lake in Central Europe*, H. Löffler, Ed. (Junk, The Hague, Netherlands, 1979), pp. 337–384.
74. D. Riedel, *Arch. Hydrobiol.* **58**, 435 (1962).
75. M. Burgis *et al.*, in *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska, Eds. (Polish Scientific, Warsaw, 1972), pp. 301–309.
76. J. Sarvala, *Luonnon Tutkija* **78**, 181 (1974).
77. M. A. Hatanaka, in *Productivity of Biocenoses in Coastal Regions of Japan*, K. Hogetsu, M. Horanaka, T. Hatanaka, T. Kawamura, Eds. (Japanese Committee for the International Biological Program Synthesis, Tokyo, 1977), vol. 14, pp. 173–221.
78. P. Ohm and H. Remmert, *Vie Milieu* **6**, 194 (1955).
79. K. Aulio *et al.*, *Sakylan Pyhajarven Tila* (Lounais-Suomen R.Y., Turku, Finland, 1981).
80. H. M. Wilbur, *Ecology* **53**, 3 (1972).
81. T. Mizuno and J. I. Furtado, in *Tasek Bera*, J. I. Furtado and S. Mori, Eds. (Junk, The Hague, Netherlands, 1982), pp. 357–359.
82. K. Hogetsu, in *Marine Production Mechanisms*, M. J. Dunbar, Ed. (International Biological Programme Series, no. 20, Cambridge Univ. Press, Cambridge, England, 1979), pp. 71–87.
83. S. W. Bradstreet and W. E. Cross, *Arctic* **35**, 1 (1982).
84. K. Kuusela, *Acta Universitatis Ouluensis* (no. 87, Oulu, Finland, 1979).
85. P. H. T. Hartley, *J. Anim. Ecol.* **17**, 1 (1948).
86. D. J. Shure, *Ecol. Monogr.* **43**, 1 (1973).
87. Y. Kitazawa, in *Ecosystem Analysis of the Subalpine Coniferous Forest of Shigayama IBP Area*, Y. Kitazawa, Ed. (Japanese Committee for the International Biological Program Synthesis, Tokyo, 1977), vol. 15, pp. 181–196.
88. L. W. Swan, *Sci. Am.* **205**, 68 (October 1961).
89. D. L. Pattie and N. A. M. Verbeek, *Condor* **68**, 167 (1966); *Northwest Sci.* **41**, 110 (1967).
90. J. Brown, *U.S. Tundra Biome 1971 Progress Rept.* (1971), vol. 1.
91. ———, Special Report, no. 2, *Biol. Pap. Univ. Alaska* (1975).
92. V. I. Osmolovskaya, *Tr. Acad. Sci. USSR Inst. Geogr.* **41**, 5 (1948).
93. T. Dunaeva and V. Kucheruk, *Byull. Mosk. Obsch. Ispyt. Prir.* **4** (no. 19), 1 (1941).
94. E. Holm and C. H. Scholtz, *Madoqua* **12**, 3 (1980).
95. P. G. Howes, *The Giant Cactus Forest and Its World* (Duell, Sloan, and Pearce, New York, 1954).
96. I. K. Sharma, *Trans. Indian Soc. Desert Technol. Univ. Center Desert Stud.* **5**, 51 and 77 (1980).
97. E. A. Shushkina and M. E. Vinogradov, in *Marine Production Mechanisms*, M. J. Dunbar, Ed. (International Biological Programme Series, no. 20, Cambridge Univ. Press, Cambridge, England, 1979), pp. 251–268.
98. T. S. Petipa, *ibid.*, pp. 233–250.
99. B. A. Menge *et al.*, *Oecologia (Berlin)* **71**, 75 (1986).
100. D. C. Edwards, D. O. Conover, F. Sutter, *Ecology* **63**, 1175 (1982).
101. P. W. Glynn, *Beaufortia* **148** (no. 12), 1 (1965).
102. C. H. Peterson, *Oecologia (Berlin)* **39**, 1 (1979).
103. W. G. Hewatt, *Am. Müll. Nat.* **18**, 161 (1937).
104. J. C. Castilla, *Medio Ambiente* **5**, 190 (1981).
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Transposon Tagging and Molecular Analysis of the Maize Regulatory Locus *opaque-2*

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Genetic analyses suggested that the *opaque-2* (*o2*) locus in maize acts as a positive, trans-acting, transcriptional activator of the zein seed storage-protein genes. Because isolation of the gene is requisite to understanding the molecular details of this regulation, transposon mutagenesis with the transposable element *suppressor-mutator* (*Spm*) was carried out, and three mutable *o2* alleles were obtained. One of these alleles contained an 8.3-kilobase autonomous *Spm*, another a 6.8-kilobase nonautonomous *Spm*, and the third an unidentified transposon that is unrelated to *Spm*. A DNA sequence flanking the autonomous *Spm* insertion was verified to be *o2*-specific and provided a probe to clone a wild-type allele. Northern blots indicated that the gene is expressed in wild-type endosperm but not in leaf tissues or in endosperms homozygous for a mutant allele of the *O2* gene. A transcript was detected in endosperms homozygous for mutations at *opaque-7* and *floury-2*, an indication that *O2* expression is independent of these two other putative regulators of zein synthesis.

THE ZEIN STORAGE PROTEINS OF maize constitute a family of approximately 15 to 22 polypeptides. By SDS-polyacrylamide gel electrophoresis they can be separated into two major size classes of approximately 22 and 19 kD (*I*). Synthesis of all zein polypeptides in the endosperm is coordinately regulated, beginning at 12 days after pollination (DAP) and peaking at about 22 to 25 DAP. Zein proteins are sequestered in protein bodies derived from the endoplasmic reticulum, and translation of zein messenger RNA (mRNA) is accomplished by polysomes located directly on the surface of these protein bodies (2). At seed maturity zeins may represent 60% or more of the total protein (3).

Several mutations that decrease the amount of zein in the seed have been described (1). In contrast to wild-type kernels that have hard, translucent endosperms, mutant kernels have endosperms that are soft and opaque. One of these mutations, *opaque-2* (*o2*), can result in a 50 to 70% reduction in zein content (3). In some inbred strains—for example, Oh43, W22, or W64A—the 22-kD class of zeins is affected substantially more than the 19-kD class. In plants homozygous for *o2*, this selective decrease cannot be attributed to defects in synthesis, transport, or protein processing but is rather the result of a deficiency in the zein mRNA's for the 22-kD subgroup (4).

Genetic linkage analysis has placed the *o2* locus on the short arm of chromosome 7, whereas several of the genes for the 22-kD zeins have been mapped to chromosomes 4 and 10 (*I*). Although a few zein structural genes have been mapped to the same chromosome arm as *o2*, they are not the ones affected by *o2* mutations. These results suggest that the *O2* gene is a trans-acting regulator of zein expression. At the molecular level, the nature and complexity of the role that *O2* plays in zein expression can be addressed only after the gene is cloned.

Since the product of the *O2* gene has not been identified and is not likely to be abundant, transposon tagging appears to be the best approach to clone this regulatory locus. Two mutable alleles of *o2* have been described by Salamini and his colleagues (5): one contains a *Ds* element (nonautonomous *Ac*), and the other a novel, nonautonomous transposon that they named *Bergamo* (*Bg*). Unfortunately, neither transposon has thus far proved useful as a molecular tag; molecular probes for the *Bg* element do not exist, and molecular analysis of *Ds* insertions is complicated because DNA sequences of *Ds* elements can be very dissimilar from each other as well as from *Ac* (6, 7). Therefore, we attempted to introduce a different transposable element into the *O2* gene (Fig. 1A),

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