Increasing Turnover Through Time in Tropical Forests
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estimated for K_3C_{60} (21). The order-disorder transition in Na_2MC_{60} is thus expected to be at a somewhat higher temperature than in pristine C_{60}. Differential scanning calorimetry (22) performed on Na_2CsC_{60} between 100 and 450 K confirmed the existence of an order-disorder phase transition at 299(3) K (change in enthalpy ΔH = 2.5(5) J/g).

The fcc merohedrally disordered superconducting $M_2M'C_{60}$ compounds obey a simple monotonic relation (7) between T_c and the cubic lattice constant a. Calculations (23) using the local density approximation (LDA) with varying a showed that T_c scales well with the density of states at the Fermi level, $N(\varepsilon_F)$. The position of Na_2CsC_{60}, which adopts a different structure on the universal curve, is thus wholly fortuitous (Fig. 4). Its "normal" behavior seems to indicate that there is little effect on $N(\varepsilon_F)$ arising from the strongly modified orientational potential. This lack of effect would disagree with the conclusions of tight-binding calculations (4), which indicate that $N(\varepsilon_F)$ is higher for the $Pa\bar{3}$ structure than for the $Fm\bar{3}m$ one. A strong possibility is then that the fortuitous position of Na_2CsC_{60} on the universal curve arises from the compensating effects of a slightly reduced electron-phonon coupling constant V, originating from the stronger influence of the Na^+ ions on the ball geometry. The unexpectedly low T_c of isostructural Na_2RbC_{60} should then result from a much steeper dependence of $N(\varepsilon_F)$ or V on the intermolecular separation (Fig. 4) in $Pa\bar{3}$ compared with $Fm\bar{3}m$. Detailed discussion has to await calculations in the primitive cubic structure as well as accurate structural parameters for other sodium and lithium ternary fullerides.

A theoretical understanding of how electron hopping between neighboring fullerene molecules is affected by their relative orientation in the context of the present experimental results is essential. Its effect on the details of the band structure will determine the extent to which interfullerene interactions contribute to the superconductivity mechanism in the fullerenes in addition to the intrafullerene interactions, which strongly contribute to the pair-binding (5, 24).

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Increasing Turnover Through Time in Tropical Forests

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Tree turnover rates were assessed at 40 tropical forest sites. Averaged across inventoried forests, turnover, as measured by tree mortality and recruitment, has increased since the 1950s, with an apparent pantropical acceleration since 1980. Among 22 mature forest sites with two or more inventory periods, forest turnover also increased. The trend in forest dynamics may have profound effects on biological diversity.

Since the mid-20th century, a substantial body of data has been gathered on rates of tree mortality and recruitment ("turnover") in humid tropical forests. Turnover rates in mature tropical forests correlate with estimates of net productivity, as gauged by rates of basal area increment and mortality (1–3). Humid tropical forests are highly productive (4, 5), so proportional increases should be easier to detect in those systems than in temperate systems. Tropical forest study sites are also relatively secure from certain forms of anthropogenic atmospheric change such as acid precipitation (6), and their diversity buffers them against pathogen epidemics that can afflict temperate forests (7). Also, tropical forest inventory plots typically have no history of clear-felling or extractive logging; few temperate forests are old growth. Therefore, tropical forest turnover data may provide a novel test of the hypothesis that global forest productivity is increasing (8).

We compiled data on rates of tree turnover in tropical forests using logarithmic models to estimate annual mortality and recruitment rates (2). The evidence for directional change through time in tropical forest dynamics was evaluated by two methods. First, we used all forest dynamics data with ≥4 years of continuous measurement (mean, 13.3; median, 11.0; range, 4 to 38 years) and an area of ≥0.2 ha (mean, 2.7; median, 1.2; range, 0.2 to 23.5 ha) (Table 1) (9). Only forests known to have suffered mass mortality by deforestation, cyclones, drought, or flooding were excluded. The first long-term inventory that satisfied the criteria began in 1934, and measurements from the last were made as recently as 1993. The time between successive inventories of each plot was always >1 year; therefore, within each monitoring period we allocated the period's annualized turnover rate to each of the years included in the monitoring period. Using these estimates, we then compared turnover rates across all mature tropical forests through time and then separately for neotropical and paleotropical forests. Then, individual sites that have two or more successive inventory periods were used to test for temporal change within individual forests.

There has been a significant upward trend in average measured rates of turnover of tropical forest trees ≥10 cm in diameter since at least 1960 (10). One possible confounding factor is the tendency for early sites to be mostly paleotropical and for recent sites to be mostly neotropical. Within our data set, neotropical sites are more dynamic than paleotropical ones (11). Yet, when graphed separately both neotropical and paleotropical data sets continue to show significant increases in

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*1945–1993.

turnover through time, with marked accelerations in turnover in the 1980s (Fig. 1) (*12*). Although highly suggestive, these data do not prove that turnover rates have increased, because possible unequal sampling of forest types across time could skew the results within each hemisphere.

Mature forests inventoried for two or more successive periods (equal to at least three successive inventories) provide a more rigorous test of the hypothesis that tropical forests have become more dynamic, because they permit the analysis of change within sites (Table 2). These forests have also been followed longer (mean, 17.0;

Table 1. Mature tropical forests with tree dynamics data [neotropical (*21*) and paleotropical* (*17*) sites], where Lat. and long. = latitude and longitude in degrees and minutes; Elev. = elevation above mean sea level in meters; Rain = mean annual rainfall in millimeters; Plot area = area of each individual plot in that forest in hectares; Time = length of total inventory period in years; and Trees = mean number of trees ≥10 cm in diameter at breast height (DBH) per hectare. Mortality, recruitment, and turnover listed here are for trees ≥10 cm DBH, derived from survivorship and ingrowth between the first inventory and the final inventory. The logarithmic models used to estimate annual tree mortality (mort.) and recruitment (rect.) are cited in the text. Dashes represent data not recorded.

Locality, code	Lat., long.	Elev. (m)	Rain (mm)	Plot area (ha)	Time (years)	Trees (ha^{-1})	Inventory period	Mortality (% per year)	Recruitment (% per year)	Turnover (mean of mort. and rect.)
Tambopata, Peru (swamp) T1	12°49′S, 69°43′W	255	2350	0.6	7	713	83 to 90	0.70	0.94	0.82
Tambopata, Peru (alluvial) T2	12°49′S, 69°43′W	255	2350	0.95	7.75	523	83 to 91	1.84	2.83	2.33
Tambopata, Peru (old floodplain) T3	12°49′S, 69°43′W	255	2350	1	7.75	546	83 to 91	2.84	2.37	2.61
Tambopata, Peru (clay) T4	12°49′S, 69°43′W	260	2350	1, 0.4	11.7	575	79 to 91	1.97	1.96	1.96
Tambopata, Peru (sandy-clay) T5	12°49′S, 69°42′W	270	2350	1, 1	7.75	546	83 to 91	2.69	2.25	2.47
Manú, Peru (alluvial) M1	11°45′S, 71°30′W	400	2028	0.94	15.5	649	74 to 90	2.29	1.81	2.05
Manú, Peru (old floodplain) M2	11°45′S, 71°30′W	400	2028	0.3; 0.3, 1	15	669	74 to 89	2.79	2.32	2.55
Yanamono, Peru (old floodplain) YA	3°16′S, 72°54′S	140	3500	1	9.75	574	83 to 93	2.81	2.32	2.56
Mishana, Peru (sandy) MI	3°47′S, 73°30′W	140	3500	0.95	7.58	841	83 to 90	1.62	1.23	1.43
Añangu, Ecuador (floodplain) A1	0°32′S, 76°26′W	250	3244	1	8.5	417	82 to 90	3.08	—	3.08
Añangu, Ecuador (upland) A2	0°32′S, 76°26′W	315	3244	1.1	8.5	728	82 to 90	1.88	—	1.88
Añangu, Ecuador (upland) A3	0°32′S, 76°26′W	370	3244	1	4.92	734	86 to 90	1.89	1.80	1.85
Jatun Sacha, Ecuador (clay) JS	1°04′S, 77°40′W	450	4100	1	5	724	87 to 92	1.46	1.63	1.54
San Carlos de Rio Negro, Venezuela (sandy) SC	1°56′N, 67°03′W	119	3500	1	10.3	744	75 to 86	1.14	1.43	1.29
Belem, Brazil (clay) BE	1°30′S, 47°59′W	30	2760	2	15	572	56 to 71	1.84	0.81	1.33
Reserva Ducke, Brazil (clay) RD	~3°15′S, 60°W	110	2186	1, 1, 1, 1, 1	5	647	81 to 86	1.16	0.91	1.04
Nr Manaus, Brazil (clay) N1	~3°S, 60°W	~100	2186	0.64	4	—	74 to 78	1.13†	—	1.13†
Nr Manaus, Brazil (clay) N2	2°38′S, 60°10′W	~100	2000	4, 4, 4	5	—	80 to 85	1.48‡	1.50‡	1.49‡
La Selva, Costa Rica (alluvial, clay) LS	10°26′N, 83°59′W	44	3994	4, 4, 4.4	15.5	444	69 to 85	2.03	2.01	2.02
Los Tuxtlas, Mexico (upland) LT	18°36′N, 95°05′W	200	4600	0.36	7	—	75 to 83	1.06§	—	1.06§
Barro Colorado Island, Panama (clay) BC	9°10′N, 79°51′W	150	2656	2	5	414	75 to 80	1.06‖	—	1.06‖
Sepilok, Sabah (sandy) S1	5°10′N, 117°56′E	40	3150	1.81	12	655	56 to 68	1.11	1.42	1.26
Sepilok, Sabah (alluvial) S2	5°10′N, 117°56′E	15	3150	1	9.16	435	57 to 66	1.92	1.53	1.72
Lambir, Sarawak (sandy, clay) LA	4°11′N, 114°E	114	2874	0.6, 0.6, 0.6, 0.6	20.3	670	66 to 86	1.48	1.25	1.36
Mersing, Sarawak (clay) ME	2°33′N, 113°04′E	264	3905	0.6, 0.6, 0.6, 0.6, 0.6	21	438	64 to 85	1.25	1.43	1.34
Semengoh, Sarawak (upland) SE	1°36′N, 112°E	—	4167	—	21	—	60 to 81	0.89¶	—	0.89¶
Sungei Menyala, Malaysia (alluvial) SM	2°28′N, 101°55′E	30	2376	2	38	496	47 to 85	2.05	1.96	2.00
Pasoh, Malaysia (clay) PA	2°35′N, 102°19′E	90	2000	8	13	530	71 to 84	2.07	1.71	1.89
Bukit Lagong, Malaysia (ridge) BL	3°25′N, 101°42′E	505	2481	2	36	515	49 to 85	1.40	1.15	1.28
Pinang Pinang, Sumatra (andesite) PI	0°50′S, 100°20′E	550	4764	1	6.25	626	81 to 87	0.95	1.92	1.44
Gajabuih, Sumatra (shale) GA	0°50′S, 100°20′E	550	4764	0.91	7	541	80 to 87	3.27	3.36	3.32
Papua New Guinea, site 14, PN	7°40′S, ~147°E	1700	—	2	20	—	57 to 77	0.90#	—	0.90#
Queensland, Australia (granite) Q1	17°02′S, 145°37′E	730	1800	0.41	32.2	957	52 to 84	0.67	0.40	0.53
Queensland, Australia (granite) Q2	17°07′S, 145°36′E	945	1750	0.2	15.7	934	69 to 84	1.35	0.96	1.15
Queensland, Australia (metamorphic) Q3	16°47′S, 145°38′E	380	2030	0.2	12	796	69 to 81	1.11	0.68	0.89
Queensland, Australia (granite) Q4	17°05′S, 145°34′E	850	2300	1.68	17.33	816**	63 to 80	0.65**	—	0.65**
Kade, Ghana (clay) KA	6°19′N, 0°55′W	133	1640	1, 1	17	552	70 to 87	1.98	1.92	1.95
Akure, Nigeria (upland) AK	7°15′N, 5°5′E	~400	1500	23.5	25	—	34 to 60	0.67	—	0.67

*Including BC pre-drought data; excluding Bako (Sarawak), and Queensland site 5 post-disturbance data. †Trees ≥ 15.0 cm DBH. ‡Trees ≥25 cm DBH. §*Astrocaryum mexicanum* only (recruitment into adult class, mortality of adults). ‖Trees ≥ 19.1 cm DBH ¶Moraceae only, trees ≥ 16.1 cm DBH. #*Araucaria hunstenii* only. **Trees ≥10.2 cm DBH.

median, 15.0; range, 6.25 to 38 years; n = 22). Three candidate sites were excluded from statistical analyses—two that may have been affected by drought or other severe conditions before establishment (BA and Q5) and one that was heavily affected by drought during the inventory period (BC) (*13*). The remaining 19 sites are well distributed geographically (eight neotropical, eight Southeast Asian, two Australian, and one African), were established as early as 1947 and reinventoried as recently as 1993, and span most of the range of the climatic and substrate variation within the humid tropical forest biome.

We scored sites by whether annual averaged mortality and recruitment rates were higher or lower during the second inventory period than during the first. When investigators reported three or more inventory periods, we combined results from successive periods to create just two periods with as similar lengths as possible. Overall, forests experienced significantly more turnover during the second inventory period than during the first (*14*). Of the 19 sites, turnover increased in 14 and decreased in 5; the magnitude of change in 4 of the decreasing sites was very small. New inventory data for large lianas and stranglers hint of a recent trend in tropical forest structure and a possible mechanism to explain the increase in turnover: In five out of six forests, liana and strangler density has increased since 1983 (Table 3) (*15*); lianas are known to contribute to host-tree mortality (*16*).

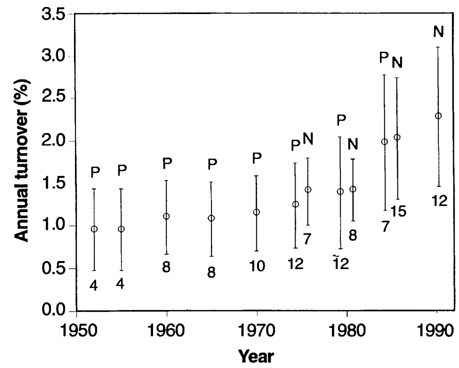

Fig. 1. Annual mean and standard deviation of all known mature tropical forest turnover rates versus year, where simultaneous $n \geq 4$ (shown below each point). Abbreviations: P, paleotropical sites (Australia, Southeast Asia, and Africa); N, neotropical sites (Central and South America). Data are for years 1952, 1955, 1960, 1965, 1970, 1975, 1980, and 1985 for paleotropical sites and 1975, 1980, 1985, and 1990 for neotropical sites. Paleotropical and neotropical data for 1975, 1980, and 1985 are plotted slightly apart to distinguish them. Numbers under the error bars correspond to the number of sites being monitored in that hemisphere during that year. See (*9*) for data sources, and see text for the calculation of turnover rates.

Humid tropical forest plots have clearly become more dynamic, suggesting a worldwide causative factor. Below, we briefly explore some candidates, related to inventory methodology and environmental change. This exploration is preliminary and speculative, but the strong signal justifies some discussion. One methodological cause of the trend might be adverse effects on tree survival from tree tagging and collecting and from soil compaction. We would expect similar time periods to elapse before any such effects were manifested; therefore, given the wide range in plot start dates, the monotonic nature of the trend indicates that this possible cause is not decisive. Some plots were deliberately located in "good-looking" forest, and an unusual predominance of large trees might be expected to show increasing turnover through time. Yet, small plots that were explicitly chosen to avoid gaps (*17*) actually slowed slightly (LA and ME), and almost all sites that were sampled randomly accelerated (for example, A1, A2, M1, M2, and SC).

Environmental change is a more likely cause. Candidates include progressively more extreme weather (for example, drought, strong wind, and temperature changes), adjacent deforestation altering local environmental conditions, and elevated productivity as a result of increased atmospheric CO_2. Although detailed site-

Table 2. Turnover of trees ≥10 cm in diameter, tropical forests with three or more inventories, where *dyn* = mean of measured mortality and recruitment, during *x* (first inventory period), and *y* (second inventory period).

Site	Plot area (ha)	Number of inventories	Time span (years)	*x*, *y*	dyn_x	dyn_y	ln (dyn_y) -ln(dyn_x)	Rank (absolute change)
BC*	2.0; 50.0	2;3	15	75 to 80, 82 to 90	1.06	2.73	0.95	1
T4	1.0	5	11.67	79 to 87, 87 to 91	1.07	2.74	0.94	2
M1	0.94	4	15.5	74 to 84, 84 to 90	1.53	2.81	0.60	3
Bako, Sarawak†	0.6, 0.6, 0.6, 0.6	5	21	65 to 75, 75 to 85	0.94	1.71	0.59	4
A1	1.0	3	8.5	82 to 85, 85 to 90	2.05	3.63	0.57	5
M2	0.3; 0.3, 1	3;2	15	74 to 84, 84 to 89	1.81	3.08	0.53	6
BL	2.0	14	36	49 to 63, 71 to 85	1.04	1.49	0.36	7
YA	1.0	4	9.75	83 to 89, 89 to 93	2.18	3.05	0.34	9
KA	1, 1	6	17	70 to 82, 82 to 87	1.76	2.44‡	0.33	10
SM	2.0	14	38	47 to 61, 71 to 85	1.59	2.13	0.29	11
GA	0.9	7	7	80 to 84, 84 to 87	2.80	3.51	0.23	12
LS	4, 4, 4.4	3	15.5	69 to 82, 82 to 85	2.02	2.50	0.21	13
SC	1.0	3	10.33	75 to 80, 80 to 86	1.17	1.40	0.18	14
Queensland site 5†	0.49; 0.28	6;6	31.9	51 to 63, 63 to 83	0.62	0.74	0.17	15
A2	1.1	3	8.5	82 to 85, 85 to 90	1.75	1.96	0.12	16
Q3	0.2	4	12.0	69 to 76, 76 to 81	0.85	0.94	0.11	17
PI	1.0	7	6.25	81 to 84, 84 to 87	1.34	1.43	0.07	19
Q1	0.41	12	32.2	52 to 69, 69 to 84	0.51	0.51	−0.00	22
ME	0.6, 0.6, 0.6, 0.6, 0.6	5	21	64 to 74, 74 to 85	1.28	1.26	−0.02	21
S2	1.0	4	9.16	57 to 61, 61 to 66	1.76	1.70	−0.03	20
LA	0.6, 0.6, 0.6, 0.6	5	20.33	66 to 76, 76 to 86	1.44	1.31	−0.10	18
S1	1.81	5	12	56 to 62, 62 to 68	1.33	0.94	−0.34	8

*El Niño–Southern Oscillation drought 1982 to 1983, first inventory of trees >19 1 cm DBH, second inventory of trees ≥30 cm DBH. †The author infers a major exogenous disturbance decades before plot establishment. ‡1982 to 1987 dynamism calculation based on differences between published 1970 to 1987 and 1970 to 1982 data.

Table 3. Available dynamics data for lianas and non–self-supporting stranglers ≥10 cm in diameter in mature tropical forests.

Site	Area (ha)	Inventory period	Liana stems recruited	Liana stems died	Liana stems [start (end)]	Lianas, proportion of tree stems [start (end)] (%)
T1	0.6	83 to 90	4	0	3 (7)	0.71 (1.64)
T2	1	83 to 91	6	4	8 (10)	1.50 (1.73)
T4	1.4	83 to 91	10	1	17 (26)	2.10 (3.11)
T5	2	83 to 91	13	6	31 (38)	2.84 (3.58)
YA	1	83 to 93	11	10	28 (29)	4.88 (5.34)
MI	1	83 to 90	0	4	18 (14)	2.16 (1.74)

by-site meteorological data needed to test for weather effects on turnover are unavailable, current trends in deforestation and atmospheric change may lead to lower precipitation, increased seasonality, and more frequent extreme weather events in the tropics (*18*). Therefore, the possibility exists that tropical climate change contributed to the trend, although sites with known severe weather perturbations were dropped before analysis. Forest microclimates are also sensitive to adjacent deforestation (*19*), but short-term data only show direct biological consequences at <1 km (*20*). In contrast, ≥5 sites with accelerating turnover are >50 km from major deforestation fronts (SC, A1, A2, M1, and M2). Furthermore, it is unclear if average distances between forest plots and deforestation fronts are less now than before, because study sites have always combined primary forest status with accessibility. Therefore, edge-effect environmental change appears to be an unlikely cause of the turnover increase.

The accelerating increase in turnover coincides with an accelerating buildup of CO_2 (*21*). Increasing CO_2 concentrations may have already altered plant morphology and raised growth rates (*22*), but ecosystem effects are hard to predict. Experiments on the effects of controlled environmental change at cellular, physiological, and whole plant levels cannot be easily extrapolated to higher level phenomena like forest dynamics (*23*). For example, any effect on tree turnover by rising atmospheric [CO_2] could result as much from stimulated liana growth as from tree growth. Thus, vines show greatly enhanced growth with elevated [CO_2] (*24*) and are highly productive (*25*) "structural parasites" (*26*) known to affect tree-fall rates (*16, 27*); most tropical forests have a high liana density (*28*).

Whichever factor is most critical, the evidence suggests that even "intact" tropical forest has been affected by recent climatic and atmospheric changes. The trend to accelerated turnover has implications for global change, with likely effects on tropical biodiversity and possible unexpected links between the global carbon cycle and tropical forests. If forest turnover rates continue to increase, primary forests may become more characterized by climbing plants and gap-dependent tree species, best positioned to benefit from increased disturbance and atmospheric CO_2. Accelerating dynamics in western Amazonia (A1, A2, M1, M2, SC, T4, and YA) indicate that even the largest areas of tropical forest could become inadequate to conserve samples of the biome without the rapid reduction of carbon emissions. Although faster turnover may create a more heterogeneous forest environment, and hence enhance species richness at local scales, large-scale biodiversity levels could decline. Eventually, extinctions are possible among the slowest growing shade-tolerant tree species and among tropical forest organisms with life cycles tied to these trees. Lianas and fast-growing trees have less dense wood than shade-tolerant species (*29*). Therefore, if populations of gap-dependent species increase, primary tropical forests may increasingly become a net carbon source, rather than a sink as assumed in most recent global circulation models (*30*). Such a process would constitute an unexpected synergism between CO_2 emissions from industrialized and tropical countries.

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10. This is confirmed by a *t* test comparison of estimated 1990 turnover rates versus estimated 1960 turnover rates [t = 3.87, df = 19, P < 0.001 (one-tailed test)].
11. Statistical values: t = 1.96, df = 36, P = 0.059 (two-tailed test).
12. Within-hemisphere *t* test comparisons of estimated annual turnover confirm that forest plots in both hemispheres have become more dynamic [paleotropical: t = 2.69, 1985 versus 1960, df = 13, P = 0.009 (one-tailed test); neotropical: t = 2.64, 1990 versus 1975, df = 17, P = 0.008 (one-tailed test)].
13. This procedure was conservative: Forest turnover at all three sites accelerated, especially at BC and BA (Table 2).
14. Wilcoxon matched-pair signed-rank test, z = 2.31, df = 18, P = 0.010 (one-tailed test). At the only site with a marked decrease in turnover (S1), it appears likely that recruitment in the final inventory period was incompletely recorded. If this site is discounted, z = 2.87, df = 17, P = 0.004 (one-tailed test). If sites last recorded before 1980 are discounted, z = 2.52, df = 16, P = 0.006 (one-tailed test).
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Magnetic Field Effects on B_{12} Ethanolamine Ammonia Lyase: Evidence for a Radical Mechanism

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A change in radical pair recombination rates is one of the few mechanisms by which a magnetic field can interact with a biological system. The kinetic parameter V_{max}/K_m (where K_m is the Michaelis constant) for the coenzyme B_{12}–dependent enzyme ethanolamine ammonia lyase was decreased 25 percent by a static magnetic field near 0.1 tesla (1000 gauss) with unlabeled ethanolamine and decreased 60 percent near 0.15 tesla with perdeuterated ethanolamine. This effect is likely caused by a magnetic field–induced change in intersystem crossing rates between the singlet and triplet spin states in the {cob(II)alamin:5′-deoxyadenosyl radical} spin-correlated radical pair.

More than 20 enzymes are thought to incorporate radical chemistry in the conversion of substrates to products (*1, 2*). Those enzymes that utilize spin-correlated radical pair intermediates should be sensitive to an applied magnetic field according to the same principles that govern radical pair chemical reactions. This proposal is not new, but it has not been substantiated by experiment until now (*3*). The only other example of a biological system that is sensitive to an applied magnetic field through electron spin selectivity is the triplet yield and emission intensity of the bacterial photosynthetic reaction center (*4*). Through a mechanism other than spin-correlated chemistry, integral membrane enzymes may couple to the electric field vector of an alternating electromagnetic field. This process does not require radical chemistry, and it is limited to membrane-bound proteins that undergo large conformational changes during catalysis (*5*).

The rate or product distribution of chemical reactions that involve geminate radical pair or biradical intermediates can be altered by a magnetic field that increases or decreases intersystem crossing (ISC) rates between the singlet and triplet spin-correlated states (*6*). A geminate radical pair born in the singlet spin state after bond homolysis will readily recombine to reform starting material. If ISC to the triplet spin state occurs, recombination to the starting material is prohibited by the Pauli exclusion principle. This results in a longer radical pair lifetime and an increased forward flux to product (Fig. 1). To allow for electron spin rephasing (ISC), a geminate radical pair must be held spatially close for 10^{-10} to 10^{-6} s. Beyond this time, interactions with solvent and neighboring atoms will lead to spin randomization. Thus, only chemical reactions that occur in this time domain may exhibit a magnetic field dependence through the radical pair spin exclusion mechanism.

The enzyme-substrate (ES) complex formally constitutes a biradical or radical pair if radical character exists on both the substrate and the enzyme or cofactor at some time during the course of the reaction. If ISC occurs in the singlet ES complex to produce a triplet ES complex, the probability of nonproductive radical recombination and dissociation of S from the ES complex is decreased. The result will be an increase in the forward commitment to catalysis for the substrate (*7*). This will increase the kinetic parameter V_{max}/K_m if it occurs before the first irreversible step. If a kinetically slow event that occurs after formation of the radical pair ES intermediate requires the singlet spin state, then increased ISC will populate the three unreactive triplet spin states and V_{max} will be decreased. Conversely, if the triplet spin state is required for product formation, increased ISC will populate the triplet spin state and lead to an increase in V_{max}. These arguments are reversed if the radical pair in the ES complex is born in the triplet state, but this is unlikely in a nonphotochemical system. If the slow step is independent of the spin state of ES, V_{max} will not change, but V_{max}/K_m can still be altered by a change in nonproductive radical pair recombination.

An enzyme that requires coenzyme B_{12} (5′-deoxyadenosylcobalamin) and catalyzes a 1,2 rearrangement was chosen for study because of the ubiquitously proposed mechanism that begins with homolysis of the C–Co bond to yield 5′-deoxyadenosyl radical ($\cdot CH_2Ado$) and cob(II)alamin (Cbl^{II}) as the initial radical pair (Fig. 2) (*8*). Electron spin resonance (ESR) studies of ethanolamine ammonia lyase (EAL) with the slow substrate L-2-amino-1-propanol show evidence for two radicals (*9, 10*).

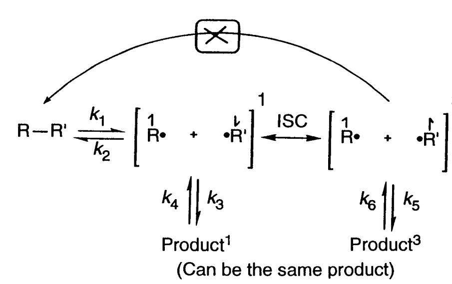

Fig. 1. Effect of a magnetic field on radical pair recombination rates in a chemical reaction.

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