blockade of PACAP38-stimulated activation of Rut–adenylyl cyclase. Thus, the NF1 protein not only acts as a negative regulator of Ras but also as a crucial component for activation of the cAMP pathway. The induced expression of a catalytic subunit of cAMP-dependent protein kinase rescues the developmental phenotype of small body size in $NF1^{P1}$ and $NF1^{P2}$ mutants (6), providing further support for the above conclusion. Exploration of the mechanism by which NF1 influences G protein–mediated activation of adenylyl cyclase may lead to new insights into mechanisms of G protein–mediated signal transduction and the pathogenesis, and possibly the treatment, of human type 1 neurofibromatosis.

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14. The larval body wall neuromuscular preparation has been described (*8, 9, 13*). The setup, saline, recording conditions, and voltage paradigms for the electrophysiological recordings were as described (*8, 9*). For recording the PACAP38-induced synaptic current, the membrane potential was clamped at −80 mV. For recording K^+ currents, command voltages were stepped from the holding potential of −80 to −50 and 20 mV, respectively. These currents include outward K^+ and inward Ca^{2+} currents, but the inward Ca^{2+} component is completely masked (*27*). PACAP38 was applied by pressure ejection through a glass electrode positioned near the voltage-clamped muscle membrane. Forskolin and cAMP analogs were applied to the solution bathing the preparation.
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26. Adenylyl cyclase activity was assayed as described (*4*) with membranes from abdomens of rut^1, $NF1^{P2}$, and wild-type flies. Calcium concentrations were calculated according to MaxChelator v1.31 (*28*). Assays were done in duplicate, and each result represents data from at least two separate experiments.
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Long-Term Responses of River-Margin Vegetation to Water-Level Regulation

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The long-term effect of water-level regulation on riparian plant communities was assessed for storage reservoirs and run-of-river impoundments. Soon after the onset of regulation, there were few species and sparse vegetation cover, regardless of whether the new water level intersected former upland or riparian vegetation. In the longer term, an impoverished vegetation was maintained by storage reservoirs, whereas in run-of-river impoundments, some community characteristics deteriorated and others recovered compared to adjacent free-flowing rivers.

Riparian ecosystems are among the most diverse systems on the world's continents (*1*) and have been suggested as sensitive indicators of environmental change (*2*). Although the majority of the world's riparian systems are affected by water regulation schemes (*3*), the long-term development of riparian communities along regulated water bodies is not known because most studies of succession after dam closure are performed on rivers which have been regulated for only a few decades (*4*, *5*). Environmental impact assessments of water regulation schemes suffer from this lack of knowledge and generally provide very little information about likely postdamming development of ecological communities. Therefore, regulations are approved without considering the chance a river's ecological integrity and biodiversity will be maintained in the long term (*6*).

We used riparian vegetation along storage reservoirs and run-of-river impoundments in central and northern Sweden to assess ecosystem readjustment after regulation (*7*). These are the two major types of regulated waters in the study area, and they are consecutive along the regulated rivers; tailwater reaches are absent or scarce. Storage reservoirs have enough capacity to offset seasonal fluctuations in water flow and provide a constant supply of water throughout the year. They have their lowest water levels in spring and their seasonal highs in summer and fall. Run-of-river impoundments provide water flow through the turbines and may store a day's or week's worth of water. The water level fluctuates daily or weekly between its statutory high and low levels throughout the year.

Depending on whether water levels were raised at the onset of regulation to intersect former upland soils or overlapped with the range of pristine water-level fluctuations, succession started either with few or many riparian species at hand. To control for this effect, we distinguished between regulated sites with preupland and preriparian land.

We sampled river-margin sites along 43 storage reservoirs and 45 run-of-river impoundments, ranging between 1 and 70 years in age. Each study site encompassed a section of river margin 200 m in length between the highest and lowest water levels during the growing season. At each site, the presence of all vascular plant species and the percentage cover of trees and shrubs and of herbs and dwarf shrubs were recorded (*8*). Species richness was then transformed (*9*) to compensate for between site variation in river-margin width, and thus study site area. We also determined height of the river margin, substrate fineness, and substrate heterogeneity (*8*). In 34 of 43 storage reservoirs, water levels were raised to increase storage capacity, and preriparian sites ($n = 9$) were too few to be treated in all analyses.

Compared to similar sites along adjacent, free-flowing rivers (*10*), the storage reservoirs had fewer species per 200-m length of river margin (58 versus 83 species; $P < 0.0001$, Mann-Whitney U test) and a lower transformed species richness (57 versus 95 species, $P < 0.0001$). The corresponding figures for run-of-river impoundments were 74 versus 87 ($P = 0.0032$) and 97 versus 97 ($P = 0.71$). Thus, after nar-

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rowing of the river margins following reduction of water-level ranges, species numbers differed but species concentrations did not.

To assess variation in transformed species richness with age of regulation, we performed locally weighted regression scatterplot smoothing, or LOWESS regression (Fig. 1) (*11*). In preupland sites along storage reservoirs, transformed species richness increased during the first 34 years after dam closure, but decreased thereafter (Fig. 1). Along run-of-river impoundments, preupland sites had maximum species richness at about 13 years, and preriparian sites at about 18 years after dam closure (Fig. 1). The same analysis on untransformed species-richness data resulted in covarying curves. Although some species have various adaptations to resist flooding (*12*), the low initial values and subsequent increases of transformed species richness, indicate that vegetation was largely destroyed during the first year of impoundment, regardless of where regulated river margins were located.

Along storage reservoirs, transformed species richness was slightly higher on preriparian than on preupland sites, but the difference was not statistically significant ($P = 0.060$, Mann-Whitney *U* test; Fig. 1). Along run-of-river impoundments, the preriparian sites had more species ($P = 0.019$; Fig. 1). It cannot be inferred whether this difference between types of sites was because preupland sites were more strongly disturbed or because dispersal limitation restricted recruitment after plant mortality at the onset of regulation. In any case, the LOWESS lines were similar for the two types of sites along the run-of-river impoundments (Fig. 1), suggesting that successional pathways were similar as well.

For preupland sites along storage reservoirs, transformed species richness was significantly correlated with substrate fineness ($r = 0.41$, $P = 0.016$, Spearman's coefficient of rank correlation). Along run-of-river impoundments, preupland sites showed no statistically significant correlations between transformed species richness and environmental variables ($P > 0.05$), but in preriparian sites, transformed species richness was significantly correlated with substrate fineness and riverbank height (with $r = 0.48$ and $P = 0.011$, and $r = 0.50$ and $P = 0.015$, respectively).

To eliminate the effect of soil texture, we performed a regression with transformed species richness as the dependent variable and substrate fineness as the independent variable and plotted the residuals against age of the regulated water bodies. However, the relationship between transformed species richness and time retained the same pattern, indicating that changes represented succession and not differences in soil among shorelines. Substrate heterogeneity was not significantly correlated ($P > 0.05$, Spearman's coefficient of rank correlation) with transformed species richness and is unlikely to have confounded successional patterns.

Along the storage reservoirs, values of vegetation cover remained constantly low after regulation and were not significantly influenced by site origin ($P > 0.05$, Mann-Whitney *U* tests). Most plants were confined to a narrow zone at the top of the river margin. Along the run-of-river impoundments, vegetation cover showed a change with time similar to that of transformed species richness. Furthermore, preriparian soils had a higher cover of herbs and dwarf shrubs than did preupland soils ($P = 0.0030$), but the cover of trees and shrubs did not differ significantly ($P > 0.05$) among types of sites.

The transient recovery of species richness for both kinds of water bodies (Fig. 1) suggests that regulated water-level regimes were not the only governing factors. Physical factors such as erosion of fine grade substrates, including nutrient release, may have been important, as suggested by the correlations between transformed species richness and substrate fineness and other evidence (*13*). Although substrate fineness did not change with time on the scale of 200-m reaches ($P > 0.05$), a successive redistribution of fine grade soils from upper to lower levels of the river margin (*14*), that is from more to less vegetated ground, could have affected results. Reduction of the available species pool because of constraints on dispersal after fragmentation of the river corridor by dams is also likely to have played a role (*15*).

Regardless of changes in species richness after regulation, the regulated sites could have developed a different species composition than free-flowing sites. We tested for floristic recovery with time by comparing the species composition of the oldest 50% of the regulated sites (that is, within the range of 20 to 70 years) with free-flowing sites (*10*), using Detrended Correspondence Analysis (DCA) (*16*). The mean sample scores differed between the sites along regulated and free-flowing rivers for both the first (123.6 versus 86.9), second (87.1 versus 109.6), and third (72.5 versus 90.7) DCA axes ($P < 0.001$, $P = 0.012$, and $P = 0.010$; *t* tests) for old preupland sites along storage reservoirs ($n = 17$). The scores also differed for the first (161.0 versus 97.4) and second (103.7 versus 73.9) DCA axes for old preupland sites along run-of-river impoundments ($P < 0.001$ and $P = 0.006$; $n = 10$), suggesting that regulated and free-flowing sites maintain different floras in the long term. However, for old preriparian

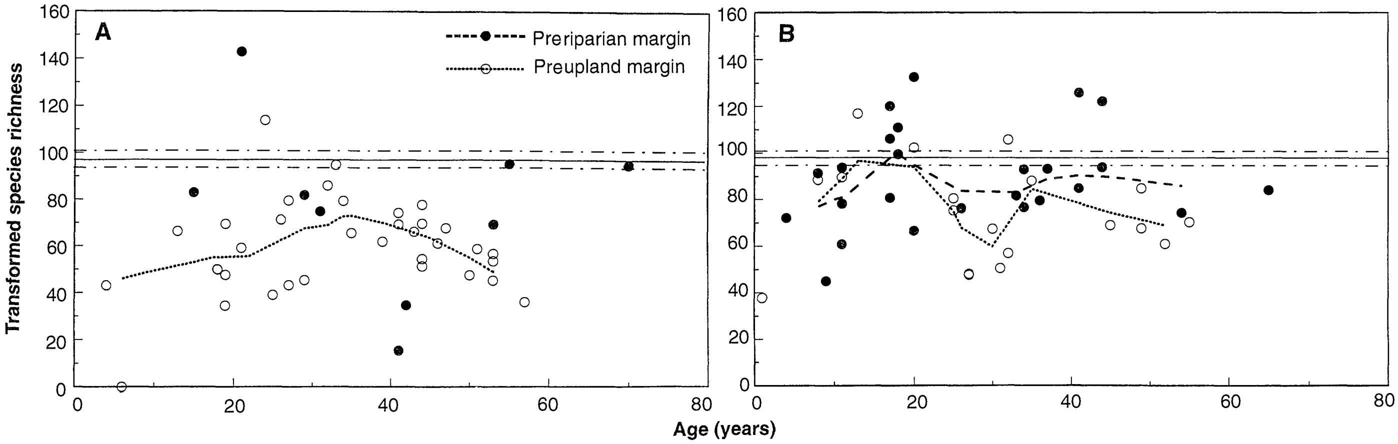

Fig. 1. Development of species richness is shown for riparian vegetation of vascular plants along (**A**) storage reservoirs and (**B**) run-of-river impoundments in central and northern Sweden. Values have been transformed to compensate for between-site differences in river-margin width, but all sites comprise stretches of river margin 200 m in length between the regular high- and low-water levels of the growing season. Curves were smoothed with LOWESS regressions. The mean values (and 95% confidence intervals) of transformed species richness for adjacent, free-flowing rivers (*10*) are indicated by horizontal lines.

sites along run-of-river impoundments (n = 13), the mean sample scores for the first DCA axis did not differ from those of free-flowing sites (115.8 versus 102.7, $P = 0.095$), suggesting that floristic recovery may occur.

To conclude, the storage reservoirs developed a river-margin vegetation that is permanently different from that in free-flowing rivers. In run-of-river impoundments, some floristic variables deteriorated, whereas others recovered in the long term, supporting the contention that fragile and resilient qualities may be combined in a single community (*17*). Our results have implications for river management. First, impounding boreal rivers for hydroelectric purposes, thus changing naturally sloping rivers to stairs of dams and level water bodies and offsetting seasonal fluctuations in flow, will obstruct the maintenance of species diversity. Second, accurate assessments of community responses to hydrological disruption of rivers require multivariate approaches. Given that the majority of the world's rivers are regulated (*3*), the results may raise the requirements on future dam licensing and relicensing to modify dam operation in such ways that ecological effects might be alleviated (*18*).

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7. In the storage reservoirs, live storage capacities ranged between 8.6 and 5900 Mm^3, water-level fluctuations ranged between 1.3 and 34.5 m during the growing season, and corresponding shoreline widths were between 8.3 and 700 m. In the run-of-river impoundments, water-level fluctuations ranged between 0.3 and 2.5 m during the growing season, and bank widths between 0.3 m and 70 m. The Lule, Pite, Skellefte, Ume, Ångerman, Indal, Ljungan, and Ljusnan rivers were chosen for study. These rivers all rise in the mountain chain that forms the border between Norway and Sweden and empty into the Gulf of Bothnia. Regulated water bodies on the rivers were systematically chosen to control for variation in location, size, and age of regulation, and exact site locations within water bodies were randomly chosen along their northern side.
8. The definition of a species follows T. O. B. N. Krok and S. Almquist [*Svensk Flora: Fanerogamer och Ormbunksväxter* (Esselte, Uppsala, Sweden, ed. 26, 1984)]. Percentage cover was estimated for trees and shrubs (>0.25 m), and for dwarf shrubs (<0.25 m) and herbs. Bank height was measured as the vertical distance between the highest and lowest water levels during the growing season. Substrate types were classified according to particle size into peat, clay, silt, sand, gravel, pebbles, cobbles, boulders, and bedrock. Substrate fineness was calculated by weighing values of mean particle size by percentage composition of the river margin substrate, and substrate heterogeneity was calculated as the total number of substrate types at each site [C. Nilsson, G. Grelsson, M. Johansson, U. Sperens, *Ecology* **70**, 77 (1989)].
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Defective Excitation-Contraction Coupling in Experimental Cardiac Hypertrophy and Heart Failure

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Cardiac hypertrophy and heart failure caused by high blood pressure were studied in single myocytes taken from hypertensive rats (Dahl SS/Jr) and SH-HF rats in heart failure. Confocal microscopy and patch-clamp methods were used to examine excitation-contraction (EC) coupling, and the relation between the plasma membrane calcium current (I_{Ca}) and evoked calcium release from the sarcoplasmic reticulum (SR), which was visualized as "calcium sparks." The ability of I_{Ca} to trigger calcium release from the SR in both hypertrophied and failing hearts was reduced. Because I_{Ca} density and SR calcium-release channels were normal, the defect appears to reside in a change in the relation between SR calcium-release channels and sarcolemmal calcium channels. β-Adrenergic stimulation largely overcame the defect in hypertrophic but not failing heart cells. Thus, the same defect in EC coupling that develops during hypertrophy may contribute to heart failure when compensatory mechanisms fail.

Hypertensive disease can lead to cardiac hypertrophy and heart failure and is a major cause of death in developed countries. The heart failure that follows prolonged hypertension is characterized by decreased cardiac contractility and ejection fraction with sequelae that include pleural effusions, ascites, hepatic congestion, and atrial thrombi (*1*). Animal models of hypertension, cardiac hypertrophy, and heart failure show that pressure overload leads first to hypertrophy and then to a loss of contractile function (*1*, *2*). In healthy heart-muscle cells, electrical excitation leads to contraction because depolarization of the cardiac sarcolemmal membrane opens L-type Ca^{2+} channels (or dihydropyridine receptors, DHPRs), and the resulting local intracellular Ca^{2+} concentration ($[Ca^{2+}]_i$) increase activates SR Ca^{2+}-release channels (ryanodine receptors or RyRs). This Ca^{2+}-induced Ca^{2+}-release mechanism (*3*) depends on the high local $[Ca^{2+}]_i$ in the immediate vicinity of the DHPR to rapidly activate the