OVERVIEWS

BIODIVERSITY CONSERVATION IN EUROPE AND NORTH AMERICA

I. Grasslands

A Common Challenge

By David A. Wedin

Conservationists on both sides of the Atlantic face losses in biodiversity resulting from fragmentation, changing disturbance regimes and increasing eutrophication.

Only 200 years ago the North American tallgrass prairie was a vast natural system shaped by climate, topography, fire and herbivores. Today it is almost gone. In Iowa only a few thousand hectares of an original 12 million hectares of prairie remain (Cooper, 1982). Across the Midwest, the prairie persists as rare, isolated fragments in a landscape dominated by intensive agriculture — islands threatened both by a growing variety of new anthropogenic disturbances and by the loss of processes such as fire that originally sustained them.

I recently traveled to northern Europe to visit British and Dutch ecologists working on grassland conservation and restoration. While I was excited about the prospect of seeing some of the ecological research underway there, I was not aware what relevance European experiences might have for efforts to preserve and restore tallgrass prairie in the North American Midwest. It seemed to me that the differences between the European and American situations were too great. Preoccupied by the plight of the tallgrass prairie, I assumed there could be no comparable situation in Europe. In the course of my visit, I learned that I was wrong. Europeans are facing problems strikingly similar to ours, and the lessons they have learned trying to cope with these problems are applicable in North America.

Two stereotypes initially prevented me from seeing the relevance of European grassland conservation to the tallgrass prairie. The first was the notion that an equilibrium between people and nature exists in Europe. When Americans think about the European landscape, they imagine a balance between towns, agricultural fields and semi-natural areas that goes back for centuries. Clearly no such equilibrium exists in North America, where vast portions of the original landscape have been dramatically altered within the last century.

At first glance, much of the landscape in northern Europe supports this impression. The pastoral landscape of this area, with its small fields, hedgerows, sheep-grazed meadows, windmills and quaint villages, is superficially similar to the Europe that 19th century emigrants left for America. This superficial similarity, however, is a devastation of European natural areas and a loss of biodiversity during the past century that has actually been just as dramatic as anything seen in North America. According to Jan van Groenendael, a plant ecologist at the Dutch Agricultural University at Wageningen, Holland has lost 30 percent of its plant species during the last century. And in Britain, ten vascular plant and four invertebrate species have gone extinct during the same period; another 149 plant and 14 invertebrate species are endangered (Green, 1990).

This loss of biodiversity was also evident when I traveled across southern England with a group of British and Dutch ecologists. One of the communities we visited was a species-rich fen dominated by purple moor grass (*Molinia caerulia*) and meadow thistle (*Cirsium dissectum*), together with several dozen ericads and forbs. Devon,

British and Dutch ecologists examine an ancient wet meadow near Oxford, England, during a recent tour. Like many other European grassland types, wet meadows have dwindled rapidly in recent decades, and attempts to find ways of restoring them are leading to important insights into their origins and ecology. *Photo by David Wedin*

in southwest England, has lost 95 percent of this vegetation type since World War II. In the last five years alone, the extent of this community has decreased 65 percent, according to Jerry Tallowin of the Institute for Grassland and Environmental Research at North Wyke. This fen type was also once common in the Netherlands, where, according to Jan van Groenendael, less than 50 hectares remain in the entire country. This story is repeated for many of northern Europe's species-rich communities, particularly grasslands, heathlands and peatlands. The threats to grassland biodiversity and the conservation problems in Europe appear to be just as serious as those in North America. Just as in the American Midwest, conservationists in northern Europe are left trying to preserve, maintain and restore tiny fragments of these threatened communities in an increasingly agricultural and urban landscape.

My second stereotype was that because the species-rich ancient grasslands of northern Europe are anthropogenic rather than natural, they would contain fewer species—in particular fewer rare and endemic species, and have less significance for conservation than natural grasslands. Although the presettlement vegetation of much of Britain and Europe was forest, most of these forests were destroyed in the Neolithic Era, and the remainder have been heavily influenced by civilization (Tansley, 1939; Bakker, 1989; Green, 1990). Rackham (1980) estimated that in 1086, when the first systematic land survey of England was done, only 15 percent of England's land area remained in forest. The ancient grasslands that replaced the forests have been maintained by mowing, grazing, sod-cutting, and fire for millennia (Bush and Flenley, 1987). Defined in a broad sense, these ancient grasslands include chalk grasslands, meadows, heathlands, fens, moors and other related communities. How could the conservation of these managed pastures and hayfields have the same significance to global biodiversity as preserving and restoring a natural system such as the tallgrass prairie?

This assumption was unwarranted. "Natural" or not, the ancient grasslands of Europe are incredibly rich in species. The species richness of these ancient grassland communities is often 30-40 vascular plant species per square meter (Bakker, 1989). In contrast, Peet et al. (1983) report that, on average, North American tallgrass prairie contains only 18 vascular plant species per square meter. The Drentsche A nature preserve in northern Holland consists of a few thousand hectares with relatively subtle topographic and edaphic variation, yet it contains over 500 vascular plant species (Bakker, 1989). Moreover, the ancient European grasslands include many endemic species in contrast to the tallgrass prairie, which has very few endemics (Wells, 1970). The grasslands of northern Europe have distinct sets of species adapted to different combinations of conditions and disturbances, and include many endemic plants and invertebrates (Tansley, 1939; Scholz, 1975; Ellenberg, 1978; Green, 1990). This leads to a high diversity of both species and communities on the landscape level.

And if the ancient European grasslands are more "natural," or at least more significant in terms of biodiversity, than I first thought, the tallgrass prairie may actually be less "natural" than we realize (Steuter, 1991). The tallgrass prairie appears to be a relatively derived community that arose in less than ten thousand years after the last glaciation and that is composed largely of species with origins elsewhere (Axelrod, 1985). In fact, like the European grasslands, it may have been shaped and maintained in part by human beings (Steuter, 1991; Axelrod, 1985).

My point is not that tallgrass prairie conservation is unimportant. Rather, it is that our preoccupation with "naturalness" affects how we set our conservation goals, how we determine what is worthy of protection or restoration, and what management tools we decide are appropriate or inappropriate. The British scientist Robert Boyle (1686) declared that it is an "unhappy thing...that the word nature hath been so frequently and yet so unskillfully employed." Not only is the concept of "naturalness" vague, it may sometimes stand in the way of efforts to conserve biodiversity. It was evident in my visit that European conservation biologists and natural areas managers are struggling with this concept of "naturalness" just as North Americans are.

Lessons from Northern Europe

Many species-rich communities are endangered in northern Europe. In this note I will concentrate on several types of ancient grasslands: chalk grasslands, wet meadows and heathlands. For these examples, I will consider why the community currently faces such serious threats, how both basic ecological research and early attempts at restoration have furthered the understanding of these species-rich communities, and how these insights are useful to North American ecologists and conservation biologists.

Some of the best-known ancient grasslands in Europe are calcareous grasslands, which include the chalk grasslands, limestone pavements, and alvars. These grasslands occur on thin, infertile soils overlying calcareous bedrock, and appear to have been maintained by grazing (usually by sheep) for hundreds, if not thousands, of years (Bush and Flenley, 1987). The Salisbury Plain, site of Stonehenge in southern England, was once an extensive region of chalk grassland, but only tiny fragments of its original grasslands remain. These remnants, however, support a diverse biological community containing numerous threatened plants and invertebrates. Approaching Wyle Down, a nature preserve near Salisbury, in early May we were first struck by the brilliant yellow of the abundant cowslips (*Primula veris*) and the purple of early purple orchids (*Orchis mascula*). When we examined the sward more closely, we found that the closely-cropped vegetation was densely packed with both forb and grass species, most not in flower at the time. Scattered across the site were numerous rabbit warrens, a high density of rabbit pellets, cattle dung from the previous growing season, and scattered shrubs. Collapsed rabbit warrens were covered by a mat of forbs less than 1 cm thick that included species of the genera *Stellaria* and *Cerastium*. Some spots had a dozen species in a 10cm by 10cm square—a patch the size of a hand.

Charlie Gibson of Imperial College described three phases in the loss of British chalk grasslands over the last century. As was the case for North American tallgrass prairie, the obvious threat to the chalk grasslands has been the plow. Just as important in their disappearance, however, have been changes in historic disturbance regimes. In the 1870s, a major economic depression led to decreased sheep grazing on these relatively unproductive grasslands as low prices for mutton and wool made the labor-intensive herding of sheep in these areas unprofitable. In the absence of grazing, the chalk grasslands were rapidly invaded by shrubs and trees. To some degree, the grazing pressure on these areas was maintained by high rabbit populations. However, in the 1950s myxomatosis severely reduced the number of rabbits in Britain, and the invasion of chalk grasslands by woody species has accelerated since then.

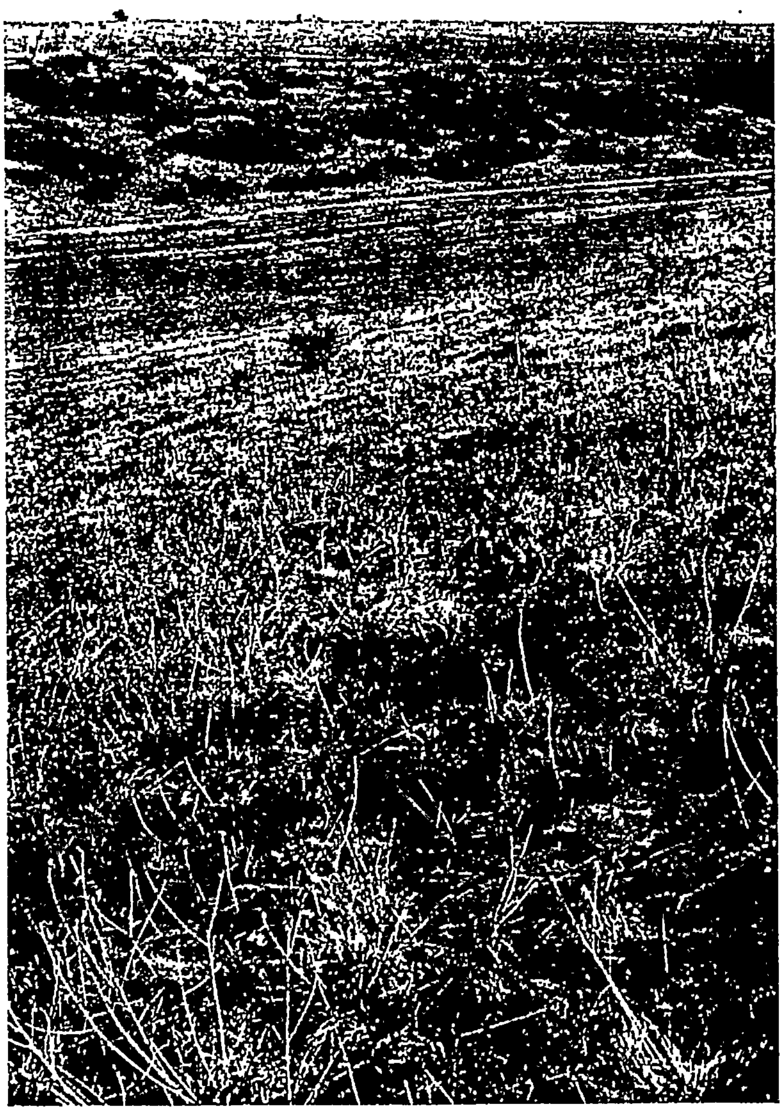
A second phase in the disappearance of the ancient chalk grasslands began in the 1910s when large areas were converted to cropland to meet the grain needs of Britain during World War I. Extensive conversion of grassland to cropland continued during and after World War II. Standing on a ridge near the Wyle Down Preserve today, one looks across the Salisbury Plain and sees thousands of hectares of cropland that were chalk grassland less than a century ago.

The most recent phase in the demise of the ancient grasslands has been the intensification of grassland agriculture in the last few decades (Green, 1989, 1990). Dramatic increases in the use of chemical fertilizers and herbicides have greatly increased the productivity of the grasslands (Ball and Ryden, 1984; Van Der Meer et. al., 1986). However, this management has also led to sharp decreases in the species diversity of grasslands and a shift in dominance from short tussock grasses such as sheep's fescue (*Festuca ovina*) to highly productive species such as perennial ryegrass (*Lolium perenne*) (Bobbink, 1991). European ecologists commonly refer to this as eutrophication—a term that North Americans have usually applied only to aquatic habitats. The result is the same in both terrestrial and aquatic habitats, however: dramatic increases in productivity, the invasion of new dominant species (often noxious or of little value to native fauna), and a precipitous drop in species diversity. The impact of fertilization on grassland biodiversity should not be surprising; the pattern of decreasing species richness with increasing productivity is one of the best-documented relationships in plant ecology (Grime, 1979; Silvertown, 1980a; Tilman 1982). For economic reasons, the European farmer must choose between "improving" his infertile, ancient grasslands or ignoring them. "Improvement" means the addition of fertilizer and the elimination of forbs with herbicides. Ignoring these chalk grasslands means stopping an archaic and unprofitable grazing or mowing regime. Either way, the result is the rapid loss of the ancient, diverse grassland (Green, 1990).

What about attempts to restore these grasslands? Results of a few experiments suggest that it may be possible, given suitable conditions and time. Outside of Oxford, we visited Wytham Woods, where Charlie Gibson and Val Brown of Imperial College are doing chalk grassland research. Their research site is an abandoned field in a woodland area containing outcrops of limestone bedrock and small pockets of unplowed chalk grassland. Brown and Gibson are studying the roles of sheep grazing, seed dispersal, and invertebrate dispersal in the recovery of a species-rich chalk grassland community on the site. Since the site was last plowed ten years ago, the reinvasion by both plant and insect species has been slow and sporadic. In other sites, which lack nearby intact chalk grasslands as seed sources, the recovery of species diversity is even slower. Recruitment of new species is also dependent on gaps in the cover of dominant grasses. Attempts to restore locally extinct forb species by simply adding seed have usually failed unless grazing or some other disturbance was also used to create gaps, according to Jonathan Silvertown of the Open University at Milton Keynes (Silvertown, 1980b). Both groups have concluded that soil conditions are important. If site fertility has been increased by fertilizer additions, the recovery of high species diversity is much more difficult (see also Wells, 1980; Bobbink, 1991).

A second group of endangered ancient grasslands that were once common across northern Europe includes a variety of wet meadows maintained either by annual hay cutting or haying together with grazing. As with chalk grasslands, the ancient wet meadows typically have a high species diversity with distinctive community types reflecting variations in disturbance regime, soil type and hydrology (Tansley, 1939; Ellenberg, 1978; Bakker, 1989). Because these wet meadows are very productive if fertilized, few of them have escaped the intensification of grassland agriculture in the last few decades. This is especially true in Holland, where farmers use high nitrogen-application rates to maximize grass production and support a large dairy industry on a small land area (Van Der Meer, 1986). The result, of course, is a shift in the dominant species and sharp declines in plant species diversity (Bakker, 1987, 1989).

Recent developments, however, have created opportunities for restoration of these communities. During the last few years, large areas of grassland have been taken out of intensive production in both Britain and Holland, a process European ecologists have termed grassland extensification. This is occurring for three reasons: first, the need to reduce the surplus production capacity for milk and other commodities caused by improvements in technology and changes in agricultural trade practices; second, realization of the environmental effects of intensive agriculture, such as declining groundwater quality; and third, the need to preserve threatened biodiversity (Van Der Meer, 1986; Green 1989, 1990). The situation clearly is an opportunity and a challenge for restorationists. The question, as Jan Bakker, a plant ecologist at the University of Groningen in Holland, put it, is "is there a way back from degraded grasslands to species-rich grassland communities?".



Chalk grasslands like this one at Wyle Down nature preserve near Salisbury in southern England frequently rival or even exceed North American prairies in species richness. Here the rich vegetation of this ancient system contrasts with the monotony of "improved" grassland on the lower land beyond—and also with an area being invaded by woody vegetation in the absence of grazing on the opposite hillside. *Photo by David Wedin*

The first attempts to restore these species-rich wet meadows stressed restoration of historic grazing and mowing regimes. Restoring grazers and stopping fertilizer inputs failed to restore the desired community, however; productivity remained high, and species diversity remained low (Bakker, 1989). Integrated studies of plant physiology, vegetation dynamics and soil nutrient dynamics by Bakker and colleague Han Olff have since shown that the underlying problem may be changes in the availability and cycling of soil nutrients that are difficult to reverse.

Although large amounts of nitrogen are locked up in soil organic matter in the ancient wet meadows, the turnover rate of this nitrogen—in other words the rate at which nitrogen becomes available for plant uptake—was historically quite low, typically 5-10 g N $m^{-2} \cdot yr^{-1}$. Under fertilization, an extra 30 to 50 g N m^{-2} yr^{-1} was added to these grasslands. The net effect of long-term fertilization has been a large increase in both the total amount of nitrogen of the system and its turnover rate.

It turns out, moreover that cattle and sheep remove little nitrogen from the meadow system, returning most of the nitrogen they consume in plant biomass as urine and feces. Bakker and Olff hypothesize that until the availability of nitrogen is brought back down to levels near historic levels, productivity will remain high, species diversity will remain low, and efforts at restoration will fail. Bakker also stressed that the wet meadows are also quite sensitive to hydrologic changes caused by changes in drainage of adjacent agricultural land. Because the turnover rate of nitrogen increases significantly if the peaty soils characteristic of these wet meadows dry out, changes in the hydrology of these meadows often compound the eutrophication caused by fertilization.

Unlike grazing, haying removes significant amounts of nitrogen from grasslands and appears to be the best strategy for countering eutrophication in fertilized wet meadows (Bakker, 1989). But even with haying, restoration of the original species-rich meadow community is a slow process. Han Olff is studying a series of fields in which fertilization has been stopped for different lengths of time. After five years of mowing and hay removal, grasses that characterize the fertilized meadows are still dominant. After 25 years of mowing, however, dominance has begun to shift to rushes (*Juncus* spp.), and species such as the broad-leaved marsh orchid (*Dactylorhiza majalis*) that are characteristic of the species-rich ancient meadows have begun to reappear. Fields that have received no fertilizer and have been mown for 45 years are approaching the species composition and diversity of the original grasslands.

Olff and Bakker acknowledged that a lack of seed sources and the absence of gaps created by grazers may ultimately limit their success in restoring these species-rich wet meadows. Once the nutrient budgets, hydrology and productivity of their wet meadows are restored, the goal is to reintroduce grazers. Unfortunately, modern Friesian and Holstein dairy cattle have been bred to require forage of such high quality that they no longer tolerate a low-quality diet of rushes, orchids, and other forbs. One solution the Dutch are experimenting with has been to import Scottish Highland cattle, which can handle the low forage quality of the unfertilized, species-rich grasslands. This breed was not historically found in Holland and so, in one sense, is not "natural" as a grazer for Dutch natural areas. On the other hand, as Han Olff pointed out, the Highland cattle may be an appropriate choice from an ecosystem function point of view.

A serious threat to northern Europe's biodiversity and an obstacle in grassland restoration efforts is the area's high rate of atmospheric nitrogen deposition (Bobbink, 1991; Cherfas, 1991). These high levels are the result of greatly increased agricultural and industrial air pollution over the last few decades. Annual atmospheric nitrogen deposition in Holland is now approximately 5 g N m^{-2} yr^{-1} (Heil et al., 1988). For many of the species-rich ancient grasslands, this may represent a doubling of their historic annual nitrogen turnover rate. Thus, even in the absence of direct fertilizer additions, signs of eutrophication are appearing in many of the ancient grassland remnants.

Elevated rates of atmospheric nitrogen deposition in combination with changes in management appear to be driving the displacement of Dutch heathlands by grasses, shrubs and trees (Heil and Diemant, 1983; Berendse et al., 1987). Historically, these heathlands were common on the infertile, sandy uplands of central Holland. They were lightly grazed by sheep, and the entire sod, including soil organic matter, roots and living plants, was harvested every 50-100 years, used as bedding in stables and barns, and then added to arable land with the manure (Bakker, 1989). Studies of the dominant heath species (*Erica tetralix* and *Calluna vulgaris*) show that they are highly adapted to a low nitrogen environment, but poor competitors under more productive conditions (Aerts, 1990). Today, because of increased productivity driven by atmospheric nitrogen inputs, soil organic matter and soil fertility in heathlands are increasing much faster than they did historically (Berendse, 1990). To maintain the dominant heath species, Dutch natural area managers now remove the entire sod on a 10-20 year cycle. Frank Berendse of the Center for Agrobiological Research at Wageningen, one of the Dutch ecologists who discovered the link between air pollution and the demise of the heathlands, now fears that the management required to maintain the heathlands may be too intensive for both economic and philosphical reasons. As we watched large sod-cutting machines denuding areas the size of agricultural fields in a nature preserve, Berendse wondered "Are we just gardening to preserve species?".

Lessons for the Tallgrass Prairie

North American conservationists trying to preserve what is left of the tallgrass prairie share many problems with ecologists and managers in northern Europe. The most obvious problem is fragmentation. In the Midwest, as well as in regions such as the California central valley or eastern Washington and Oregon, most of the remaining grassland is found in small, isolated nature preserves in an agricultural landscape. The problems that fragmentation present to plant and animal populations, both in terms of dispersal and genetic viability, have been widely discussed (Saunders et al., 1991).

A second threat to grassland biodiversity on both continents has been the loss of the historic disturbance regimes that originally maintained these communities (Van Andel et. al., 1991). Over the last few decades, Americans working with tallgrass prairie have realized that fire must be restored if prairie remnants are to be maintained. Chalk grassland without grazing and tallgrass prairie without fire are both displaced by woody vegetation in a few decades.

It became obvious to me on my European visit, however, that another threat to grassland biodiversity is just as serious as fragmentation and the disruption of historic disturbance regimes. This is the regional change in ecosystem functioning that has occurred during the last few decades in agricultural landscapes in areas such as England, Holland or the North American Midwest. The nature of this threat is not fully understood in North America, however. Even if individual nature preserves have escaped the direct addition of modern agricultural chemicals, they cannot avoid the landscape-scale eutrophication and changes in hydrology that are a consequence of modern agricultural and industrial practices. The realization of Europeans that atmospheric nitrogen deposition is a major threat to their nitrogen-limited ancient grasslands and heathlands is highly instructive in this respect. Recent studies of the tallgrass prairie have shown both how tightly nitrogen dynamics are controlled in intact prairie, and how vulnerable the prairie is to disturbance of its characteristic nitrogen cycle (Wedin and Tilman, 1990, 1992; Tilman and Wedin, 1991; Seastedt et al., 1991). The addition of only 3 g N m^{-2} yr^{-1} to a little bluestem-(*Schizachyrium scoparium*)-dominated sand prairie in east-central Minnesota resulted in the displacement of native prairie vegetation by the non-native grasses *Poa pratensis* and *Agropyron repens* in less than a decade (Tilman, 1990). Atmospheric nitrogen deposition rates are now approaching this level in the eastern portions of the Midwest, particularly in prairie preserves near fertilized cropland (typical nitrogen fertilization rates for corn are currently about 15 g N m^{-2} yr^{-1}), feedlots, or urban air pollution sources (Wedin and Tilman, 1992). This may partly explain the invasion of prairie remnants by non-native grasses and the losses in species diversity that many managers have observed over the last few decades in the Midwest (Leach, 1991).

One of the lessons the Dutch learned from their efforts to restore their species-rich wet meadows and heathlands was that simply restoring historic disturbance regimes would not bring back the historic species-rich communities. There are good reasons to suspect that this will be true of North American prairies as well. For example, reinstating "natural" or presettlement fire regimes (assuming they can be accurately re-created) may not be sufficient to offset increases in the nitrogen availability and return the productivity of tallgrass prairie remnants to presettlement levels as input of atmospheric nitrogen continues. Attempts to reintroduce bison to Midwestern prairies will also be problematic if eutrophication of remnant or restored prairies has started to occur. Grazing will increase the already high turnover rate of nitrogen, create open sites for exotic weed invasions, and further reduce the abundance of the dominant warm-season grasses (Hobbs et al., 1991; Holland and Detling, 1990; Smith and Owensby, 1978). Here again, of course, we encounter the stumbling block of "naturalness" in determining management and restoration strategies. Although mowing and the removal of cuttings is not as "natural" as bison grazing, some type of mowing regime may be more effective at maintaining native species if the goal is to move away from frequent burning as the sole management tool.

There were other clear parallels between the European and North American conservation pictures. Many of the small nature preserves I saw in northern Europe required intensive management and may not be sustainable in the long term. Jan Bakker argued that the best way for the Dutch to use their limited conservation resources is to restore large conservation areas where they can have at least some control over landscape-level processes such as hydrology and nitrogen inputs. "Otherwise," he contends, "we're just throwing our money away on these little nature reserves". Jan van Groenendael countered, however, that "we've lost 30 percent of our plant species. In the short run we have to preserve the small remaining remnants and try to cushion them in an unfriendly landscape". The same debate is heard among conservation biologists regarding tallgrass prairie in the Midwest, some favoring a "single large area" approach emphasizing restoration and others a "several small areas" approach emphasizing preservation.

Finally, I was impressed on my visit by the strong linkages between conservation biology and agriculture in northern Europe, a situation quite different from that prevailing in North America. Many of the European ecologists I met work for or in cooperation with agricultural research stations. Roger Haggar of the British Institute of Grassland and Environmental Research, a group that traditionally focused on production agriculture, stressed that they are now addressing two problems simultaneously: the need for reductions in intensive agriculture because of overproduction and environmental degradation, and the need to preserve and enhance the habitat of threatened species and communities. Unfortunately, attempts to make agriculture more sustainable and efforts to preserve biodiversity still seem relatively unconnected in North America. The reason may lie in the types of questions asked by the two groups on this side of the Atlantic. Those working on sustainable agriculture tend to focus on ecosystem function, looking at problems such as maintaining soil organic matter and fertility, reducing soil erosion, restoring hydrological regimes, and controlling ground water pollution. On the other hand, conservation biologists have tended to focus on the population-level consequences of fragmentation and on the need to preserve or restore the species composition of threatened communities. I also suspect that the emphasis North American conservationists place on distinguishing "natural" from artificial or non-native ecosystems (see, for example, Katz, 1991) has discouraged closer ties with the agricultural community. Of all the lessons North American, particularly Midwestern, conservation biologists and restorationists can learn from recent European grassland conservation efforts, one stands out. Until we realize that finding sustainable agricultural practices and conserving threatened grassland biodiversity are intertwined problems, we may not find a solution to either.

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