PLANT TRAITS IN A STATE AND TRANSITION FRAMEWORK AS MARKERS OF ECOSYSTEM RESPONSE TO LAND-USE CHANGE

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Abstract. Understanding and forecasting changes in plant communities, ecosystem properties, and their associated services requires a mechanistic link between community shifts and modifications in ecosystem properties. In this study, we test the hypothesis that plant traits can provide such a link. Using subalpine grasslands in the central French Alps as a case study, we investigate the response of plant traits to changes in soil resource availability and disturbance regimes associated with changing grassland management as well as the effects of changes in plant traits on measured ecosystem properties. We found that fertilization leads to greater specific leaf area and leaf nitrogen content which leads to greater productivity and faster litter decomposition, and that grazing leads to higher leaf toughness and leaf dry matter content which leads to lower productivity and slower decomposition compared to mowing. A state and transition model was used as a flexible conceptual tool for integrating data on community composition, plant traits, and ecosystem properties in the context of management-mediated successional dynamics in subalpine grasslands. Focusing on the biology driving the transition between grassland states, we incorporated plant traits into the formulation of a state and transition model and demonstrated how they could be used to provide a mechanistic link between community shifts and ecosystem properties under complex management regimes with strong land-use legacies.

Key words: Central French Alps; ecosystem function; grassland traditional management; hay meadow; land-use legacies; leaf nutrient economy; litter; plant functional traits; secondary succession; subalpine grassland.

INTRODUCTION

Land-use change is a major driver of environmental and biodiversity changes worldwide (Vitousek et al. 1997, Sala et al. 2000). In Europe, seminatural ecosystems such as grasslands, steppes, heathlands, mediterranean shrublands, and savanna-type woodlands are undergoing complex land-use changes. Decreasing land-use intensity, including complete cessation of management practices is widespread, with concurrent concentration of intensive use over smaller areas that are more productive and accessible (MacDonald et al. 2000, Schmitzberger et al. 2005). In this context, understanding and forecasting changes in plant communities, ecosystem properties and their associated services requires linking community shifts and modifications in ecosystem properties using a mechanistic understanding (Chapin et al. 1997, 2000).

In European mountains, subalpine grasslands are increasingly abandoned or converted to extensive

summer grazing as traditional mowing practices disappear together with farmers and their flocks (MacDonald et al. 2000, Olsson et al. 2000, Tasser and Tappeiner 2002, Fischer and Wipf 2002, Lasanta-Martínez et al. 2005). Different management practices (fertilization, irrigation, grazing, cutting, and so on) allow for multiple combinations of resource availability (nutrients, water) and disturbance regimes (selectivity, intensity, frequency and timing of biomass destruction; sensu Grime 1979) that affect plant persistence as individuals and/or populations (Pausas and Lavorel 2003). Until 50 years ago or less, large areas of current subalpine grasslands were frequently plowed. Their long management history means that land-use legacies are an essential component of any understanding of their current dynamics (Dorioz and van Oort 1991, Tappeiner et al. 1998, Austrheim and Olsson 1999, Tasser and Tappeiner 2002). Community and ecosystem response to current management practices must therefore be set in the historical context of those practices (Foster et al. 2003).

State and transition (S and T hereafter) models (Westoby et al. 1989, Bestelmeyer et al. 2003) provide a flexible framework that can accommodate complex and changing management regimes as well as external drivers (climatic or otherwise) and are often represented as easy to grasp "box and arrow" diagrams (Allen-Diaz and Bartolome 1998, Briske et al. 2003, Bestelmeyer et al. 2004, Cingolani et al. 2005). They were developed to

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accommodate the possibility that different stable vegetation states (or none) were possible in a given location or environmental setting (Westoby et al. 1989, Bestelmeyer et al. 2003, Herrick et al. 2006). In this sense, they are complementary to earlier approaches based on "Clementsian" succession to unique climax communities (e.g., Dyksterhuis 1949). Rather than an alternative theory of vegetation dynamics, S and T models are essentially used as widely applicable, adaptative, heuristic and empirical tools for understanding and managing ecosystems (Herrick et al. 2006). Traditionally, they have focused on descriptions of communities based on dominant species and/or life forms (e.g., Bork et al. 1997, Yates and Hobbs 1997, Allen-Diaz and Bartolome 1998, Jackson and Bartolome 2002, Jasinski and Payette 2005). More recent formulations have proposed to generalize their applicability by focusing on plant functional traits and plant functional groups rather than on taxonomy (Gondard et al. 2003, Jauffret and Lavorel 2003). S and T models can also incorporate ecosystem properties as illustrated in the northern Chihuahuan desert by Herrick et al. (2002) for properties relating to rangeland health (Pyke et al. 2002) and ecosystem stability (Havstad and Herrick 2003). In this study, we used an S and T model to articulate the interlinked dynamics of plant community composition, plant traits, and ecosystem properties in response to land-use change, thereby making an essential step for a solid scientific basis to ecosystem management (Grime 2002, Stringham et al. 2003, Briske et al. 2005).

Plant traits relate to universal plant functions of growth (e.g., light and nutrient acquisition, water use efficiency) and persistence (e.g., recruitment, dispersal, defense against herbivores and other disturbances; Weiher et al. 1999). They provide a widely applicable framework for interpreting community shifts along environmental gradients (Hodgson et al. 1999, Cornelissen et al. 2003; Lavorel et al., in press). Traits related to the response of individual plants and communities to nutrient availability are also markers of ecosystem processes involved in nutrient cycling (van der Krift and Berendse 2001, Lavorel and Garnier 2002, Eviner and Chapin 2003, Garnier et al. 2004). Based on Grime's biomass ratio hypothesis (1998), changes in community composition could thus affect the dynamics of live and dead biomass (Lavorel and Garnier 2002, Chapin 2003). Garnier et al. (2004) validated these hypotheses for a set of mediterranean secondary successional ecosystems.

Based on current knowledge of plant trait responses to changing grassland management regimes, we formulated an S and T model for a subalpine grassland landscape in Villar d'Arène (Central French Alps). Our aims were to articulate alternative management practices (plowing, fertilization, cutting, and grazing) in their historical context, and to provide some functional understanding of changes in community composition and ecosystem processes in response to current and historical management. We then used this model as a framework to test two sets of hypotheses regarding the use of plant traits to simultaneously explain vegetation and ecosystem responses to management alternatives.

Our first set of hypotheses focused on vegetation response to nutrient availability and disturbance regimes as they change with land-use practices. We expect that fertilization, by increasing nutrient availability, will favor plants with higher specific leaf area (SLA; reflecting their ability to capture limiting light resources), higher concentrations of leaf nutrients such as nitrogen (leaf nitrogen content, LNC) or phosphorus (leaf phosphorus content, LPC), and with low leaf tissue density and cell wall content (leaf dry matter content, LDMC). A number of recent studies have confirmed the relevance of the nutrient acquisition/conservation trade-off governing plant nutrient economy (Díaz et al. 2004, Wright et al. 2004) to predict changes in plant communities in response to decreasing land-use intensity. These include studies across a variety of grassland types (Ansquer et al. 2004, Louault et al. 2005; S. Gaucherand and S. Lavorel, unpublished manuscript) and old fields (Garnier et al. 2004, Kahmen and Poschlod 2004). Based on existing knowledge about plant traits associated with disturbance response, we expect that conversion from cutting to selective grazing will favor grazing avoidance through small stature (Lavorel et al. 1999, Bullock et al. 2001, Stammel et al. 2003; Díaz et al., in press), protective tussock growth forms (Callaghan 1988) and lower palatability through tougher and denser leaves (LDMC; Díaz et al. 2001, Pérez-Harguindeguy et al. 2003). Colonization of post-arable soils is often seed limited (Pywell et al. 2002, Walker et al. 2004) and we expect that past plowing will have favored plants that are best equipped for long-distance dispersal and/or persistent seed bank formation (Pakeman and Small 2005, Römermann et al. 2005). On the basis of the colonization–competition trade-off in seed size (Jakobsson and Eriksson 2000, Leishman 2001, Moles and Westoby 2002), we expect species with lighter, wind-dispersed seeds to be more abundant in old fields recently ($<$50 years) converted to grasslands through spontaneous revegetation (Westoby et al. 1996, Tackenberg et al. 2003).

Our second set of hypothesis concerned the repercussions of vegetation change on ecosystem properties. We expected leaf traits that are markers of an exploitative nutrient economy (SLA, LNC; Wright et al. 2004) to translate into increased primary productivity and litter decomposition following fertilization (Lavorel and Garnier 2002, Garnier et al. 2004). Lower palatability is related to lower litter quality (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000) and we therefore expect slower ecosystem level nutrient cycling with lower productivity and higher litter accumulation in grazed compared to cut grasslands (Zeller et al. 2000).

In this paper, we first formulate an S and T model based on the analysis of coexisting historical land-use

TABLE 1. Description of 11 investigated land-use trajectories and corresponding grassland states (see Fig. 1).

Trajectory	Grassland state	Current use	*Festuca paniculata* present?	Ecosystem properties data available?
Arable rotation past use				
1	arable rotation	arable rotation	no	no
2	A1	fertilized hay meadow	no	yes
3	A2	unfertilized hay meadow	no	yes
4	B1	unfertilized hay meadow	yes	no
5	A3	grazed pasture (cattle)	no	no
6	A3	grazed pasture (sheep)	no	yes
7	B2	grazed pasture (sheep)	yes	no
Hay meadow past use				
8	C1	unfertilized hay meadow	yes	yes
9	C2	grazed pasture (cattle)	yes	no
10	C2	grazed pasture (sheep)	yes	yes
11	C2	not used	yes	no

trajectories. We then describe the abiotic and vegetation characteristics of each of the identified states, and analyze transitions among them in terms of changes in plant traits in response to the associated changes in soil resource availability and disturbance (our first set of hypotheses). Finally we analyze the role of these changes in plant traits in measured changes in ecosystem properties (our second set of hypotheses). Our results are discussed in the context of mechanisms of changes in community composition and ecosystem function and their integration into an S and T framework.

METHODS

Study site

The study site is located on the south facing aspect of the upper valley of the Romanche River, central French Alps (Villar d'Arène, 45°2′24″ N, 6°20′24″ E; see Plate 1). The substrate is homogenous calc-shale, and the climate is subalpine with a strong continental influence due to a rain shadow with respect to dominant westerly winds. Mean annual rainfall is 956 mm and the mean monthly temperatures of −4.6°C in January to 11°C in July (at 2050 m above sea level). Rainfall occurs mainly during the cooler months, with 40% of annual rainfall during the growing season.

We concentrated on the lower slopes of the study site. At the lower altitudes (1650–2000 m), former arable fields have been abandoned and subsequently converted to terraced grasslands used for hay or grazing. At mid-slope (1800–2500 m) ancient, never-plowed hay meadows are increasingly converted to light summer grazing by sheep or cattle. Some are no longer cut or grazed at all.

Putting land-use change in its historical context

We used aerial photographs from 1952, 1961, 1971, 1986, and 2001, land-use registers from 1810, 1971, and 1974, and recent data from local farmers (1996 and 2003; Association Foncière Pastorale de Villar d'Arène, *unpublished data*) to build a geographical information system (GIS) database of past and present land use.

Eighteen generic land-use trajectories were identified as successive land-use transitions between management regimes or as the continuation of a given management regime. In Villar d'Arène, these include arable rotation, fertilization, hay cutting, spring and autumn grazing, and summer grazing by cattle or sheep, among others. Trajectories thus set current land use (e.g., is the grassland cut for hay or used for summer or spring grazing by sheep or cattle?) in its historical context (e.g., has the field been plowed?). Land-use transitions relate to shifts between alternative grassland states, while stasis in a given state was hypothesized to be a result of continued identical management.

The decision to plow sets the starting point in the documented land-use trajectories (trajectory 1; Table 1). The decision to cut or graze affects both post-arable grasslands (trajectories 5, 6, and 7; Table 1) and grasslands that have never been plowed (trajectories 9 and 10; Table 1). Organic fertilization is currently undertaken on some previously unfertilized post-arable hay meadows (trajectory 2; Table 1). All the above land-use change trajectories are defined only with respect to current management (as indicated by farmer interviews, see Daigney 2005; F. Quétier, F. Rivoal, P. Marty, J. de Chazal, and S. Lavorel, *unpublished manuscript*) and past land use as available in the GIS. Hypothesizing that *Festuca paniculata,* a late-successional perennial tussock grass (see Plate 1), is an indicator of a longer time since cessation of arable rotation, we used its current presence in the field to define two additional trajectories (4 and 7; Table 1). Longer time since cessation of arable rotation is not a land-use transition as such but rather reflects our assumption of an underlying old field succession. This assumption, together with the past (plowing) and current (cutting/grazing and fertilization) differences in management defined the land-use trajectories under study, and associated land-use transitions. Land-use transitions and stases were used to formulate the S and T model. In addition, as land-use trajectories include past land use, we were able to embed current land-use changes in their historical context.

Description of land-use trajectories: resources, disturbance, and plant traits

Except for continuing arable rotation (trajectory 1), we sampled three plots per trajectory. Plots were selected as visually representative of the grassland composition found on each trajectory and distributed across the landscape to minimize spatial autocorrelation among replicates. Inter-plot variations in altitude, slope, and aspect (measured on the steepest slope of each plot) were minimized. For each plot, a 15×15 m visually homogenous area was chosen for measurement. Five land-use trajectories were investigated more thoroughly over two growing seasons (trajectories 2, 3, 6, 8, and 10) in 2003 and 2004. The remaining five trajectories (trajectories 4, 5, 7, 9, and 11) were only sampled in 2004 (see Appendix).

In each plot, 10 random soil samples (a handful) were collected in spring below the root zone (between 5 and 15 cm depth). They were mixed, sieved to eliminate rocks and stones, and analyzed for physical and chemical properties (Laboratoire d'analyse des sols, INRA, Arras, France). This sampling protocol and all that follow were agreed to within a multisite international research project (Garnier et al., *in press*). Measured variables include pH of soil solution, soil texture, and soil N, C, K, and P contents (per unit mass). Two measures of soil P were used: total P using the acid digestion method (HF; Olsen and Sommers 1982) and soluble phosphate using Olsen's procedure (Olsen et al. 1954). Soil texture and organic carbon content were used to estimate plant available water as the difference in water content between field capacity and wilting point (following Saxton et al. 1986).

Total N, P, and K contents of soils are ambiguous measures of nutrient availability for plant growth (Farruggia et al. 2003). Under non-limiting situations, N concentrations in herbaceous vegetation show a decreasing power relationship with above-ground biomass (called the N dilution curve). Although initially developed for crops (Gastal and Lemaire 2002), the N dilution curve has been validated in multi-species grasslands (Duru et al. 1997). It is the same for all C_3 plants and does not vary substantially with major environmental factors other than those affecting soil N supply (Duru et al. 1997). For a given biomass, it indicates a critical N concentration corresponding to non-limiting N availability (Gastal and Lemaire 2002). The ratio of actual N concentration to this critical concentration is called the nitrogen nutrition index (NNI), which we used to establish the degree of N limitation in each plot. Critical concentrations of P and K that maximize biomass production for a given level of N nutrition have been established (Duru and Thelier 1997). Following the same formalism, these were used to define P and K nutrition indices that identify P and K limitations for vegetation growth (PNI and KNI, respectively; Jouany et al. 2004). In this study, N, P, and K nutrition indices were calculated from living

vegetative plant parts (stems and leaves) collected before most species flowered (in mid-June). We used four random samples of 0.25 m^2 in each plot, representing an area suitable for herbaceous vegetation (Wiegert 1962).

Both mowing and grazing occur once a year. Their intensities were measured as the percentage of initial green biomass (quantified from four 0.25-m^2 above-ground standing biomass random harvests in each plot) or percentage of initial vegetative height (from 10 random measurements) remaining after disturbance, using grazing exclosures when necessary. Timing of disturbance was converted from Julian days to degree days (d.d.) based on average daily temperature measured at the study site.

Floristic composition of each plot was assessed using three nonintersecting point–quadrat survey lines (Daget and Poissonet 1969). They were 8 m long with one point every 20 cm for a total of 120 points per plot. The total number of contacts for each species was counted at each point of the point-quadrat survey. Species accounting for 80% of total abundance were identified and selected for trait measurement. Traits were measured for species $\times$ trajectory combinations as species were considered to have the same trait value across plots of the same land-use trajectory. The following quantitative plant traits were measured: plant vegetative height, plant reproductive height, leaf tensile strength (leaf toughness), leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf carbon content (LCC), and seed mass.

Leaf traits were measured on 10 individual plants per land-use trajectory, distributed evenly across the plots where they were present. Morphological traits were measured on 20 randomly selected individual plants per trajectory, distributed evenly across the plots where they were present. All these measurements followed standardized protocols (Cornelissen et al. 2003). Chemical analyses of N, P, and C contents were conducted on three samples for each species $\times$ trajectory combination, obtained by pooling the 10 original leaves sampled in the three plots of each land-use trajectory (groups of three, three, and four leaves). Two replicate analyses of C and N were carried out on each of these samples using a CHONS micro-analyzer (Carlo Erba 1500; Carlo Erba, Limito, Italy), and their values averaged. Leaf P content was analyzed using Kjeldahl mineralization. These analyses are distinct from those used to calculate the N, P, and K nutrition indices as these were done on a plot and not on a species $\times$ trajectory basis. Seed mass was measured on 100 seeds collected locally. Data on dispersal modes (anemochorous, epizoochorous, barochorous, and myrmechorous) were found in the literature and floras (Aeschimann and Burdet 1994, Lauber and Wagner 2000).

Finally, for each plot, a community aggregated trait value was calculated using the trait value of each species in the corresponding trajectory weighted according to the species relative abundance in the plot. This

aggregated trait value is a quantitative translation of the biomass ratio hypothesis (Grime 1998), whereby ecosystem properties are related to species relative abundance in a community (Garnier et al. 2004).

Description of land-use trajectories: vegetation and ecosystem properties

From the point-quadrat survey data, we calculated species number, Shannon index, and Simpson's inverse index for each plot. The total number of contacts gives an indication of vegetation density in each plot. Recorded species were classified into six a priori morphological groups following Lavorel et al. (1999). The relative abundance of the six groups (legumes, graminoids, small rosettes, small leafy stemmed dicots, large rosettes, and tall leafy stemmed dicots) was calculated.

Aboveground standing biomass was harvested in each plot at monthly intervals over the growing season (using four 0.25 m^2 in each plot). Harvest was repeated at three dates: minimum biomass around 10 May 10 (at 64 degree days), intermediate around 15 June (350 d.d.), and maximum around 10 July (635 d.d.). At each harvest, a quarter of the collected biomass was sorted into senescent and living material (including leaves, stems, and flowering stalks if present) and oven dried at 60°C for 48 h to calculate maximum standing biomass, percentage of living biomass at maximum standing biomass, aboveground net primary productivity (ANPP), and specific aboveground net primary productivity (SANPP; biomass increase per unit biomass and unit time) also called "ecosystem efficiency" (Reich et al. 1997). The same calculation was applied to changes in litter giving a specific litter net productivity (litter SANPP). The first aboveground biomass harvest of the season was used to estimate accumulated litter at snow melt.

In October 2003, a litter bag experiment was initiated in each plot using 45 polyethylene litter bags (Aerts et al. 2003). For each plot, 15 bags were filled with 1 g of a standard litter (common to all plots) and 30 bags with 1 g of litter made from senesced leaves of the plot's dominant species. Their litter was collected on the plots at the end of July 2003 and mixed in the same abundance proportions as the standing community (e.g., Knops et al. 2001). A first harvest of 15 bags (five of standard litter and 10 with litter from the plot itself) was made at snow melt in April 2004, and a second in the following autumn (October 2004). Bag contents were cleaned from soil, dried at 60°C, and weighed, giving native and standard over-winter and annual litter mass loss.

Light interception and sward height were obtained weekly over the growing season. Light interception was calculated by measuring photosynthetic active radiation (PAR) at three randomly selected locations above and below the grass cover using a 1 m long measuring rod (LI-191SA Line Quantum Sensor; LI-COR, Lincoln, Nebraska, USA). Sward height was calculated as the average of 10 random measurements in each plot. We used maximum, minimum, and snow-melt sward height in our study. By dividing light interception by maximum and minimum cover height, respectively, we were able to calculate a maximum and minimum cover density (light interception per volume of vegetation).

Statistical analysis

Making no assumptions on the normality of the data, we used non parametric Kruskall-Wallis tests to identify statistically significant differences between states for soil variables, disturbance variables, abundance of a priori morphological groups, biodiversity variables, community aggregated trait values for whole plant traits, leaf traits, reproductive traits, and ecosystem properties.

Analysis of covariance (ANCOVA) using environmental factors as covariables was performed to test hypotheses on trait response to fertilization and disturbance. ANCOVA was also used to test hypotheses on trait effects on ecosystem properties and community composition. As an example, to test whether the increase in leaf nitrogen content (LNC) following transition T2′ was the effect of the fertilization per se or was the result of an increase in light interception by the grass cover, we used maximum light interception as a covariable in testing differences in LNC between grassland states A1 and A2. These results are illustrated using box and arrow diagrams where input variables (e.g., maximum light interception) that are sufficient to account for changes in an output variable (e.g., LNC) are linked with an arrow going from the input to the output variable (see Figs. 2, 3, and 4). Statistical analyses were carried out using SPSS 11.0 (SPSS, Chicago, Illinois, USA).

RESULTS

State and transition model for seminatural grasslands in Villar d'Arène

Land-use trajectories (Table 1) were arranged into a common framework where they are interpreted as successive changes in management (corresponding to land-use transitions) initiated from either an arable rotation or a continuously cut hay meadow, and leading to contrasting grassland states (Fig. 1).

Today, arable fields could still be plowed (trajectory 1 in Table 1; "arable rotation" in Fig. 1) or constitute post arable grasslands that are cut (trajectories 2, 3, and 4 in Table 1; states A1 and A2 in Fig. 1) or grazed (trajectories 5, 6, and 7 in Table 1; state A3 in Fig. 1). Cut post-arable grasslands can be fertilized on a regular basis (trajectory 2 in Table 1; state A1 in Fig. 1) or not (trajectories 3 and 4 of Table 1; state A2 in Fig. 1). Fertilization levels are low with a local maximum of 8 to 10 Mg·ha^{-1}·yr^{-1} of farm-yard manure (Picart and Fleury 1999). Never-plowed grasslands can still be cut (trajectory 8 in Table 1; state C1 in Fig. 1), be grazed (trajectories 9 and 10 in Table 1; state C2 in Fig. 1), or
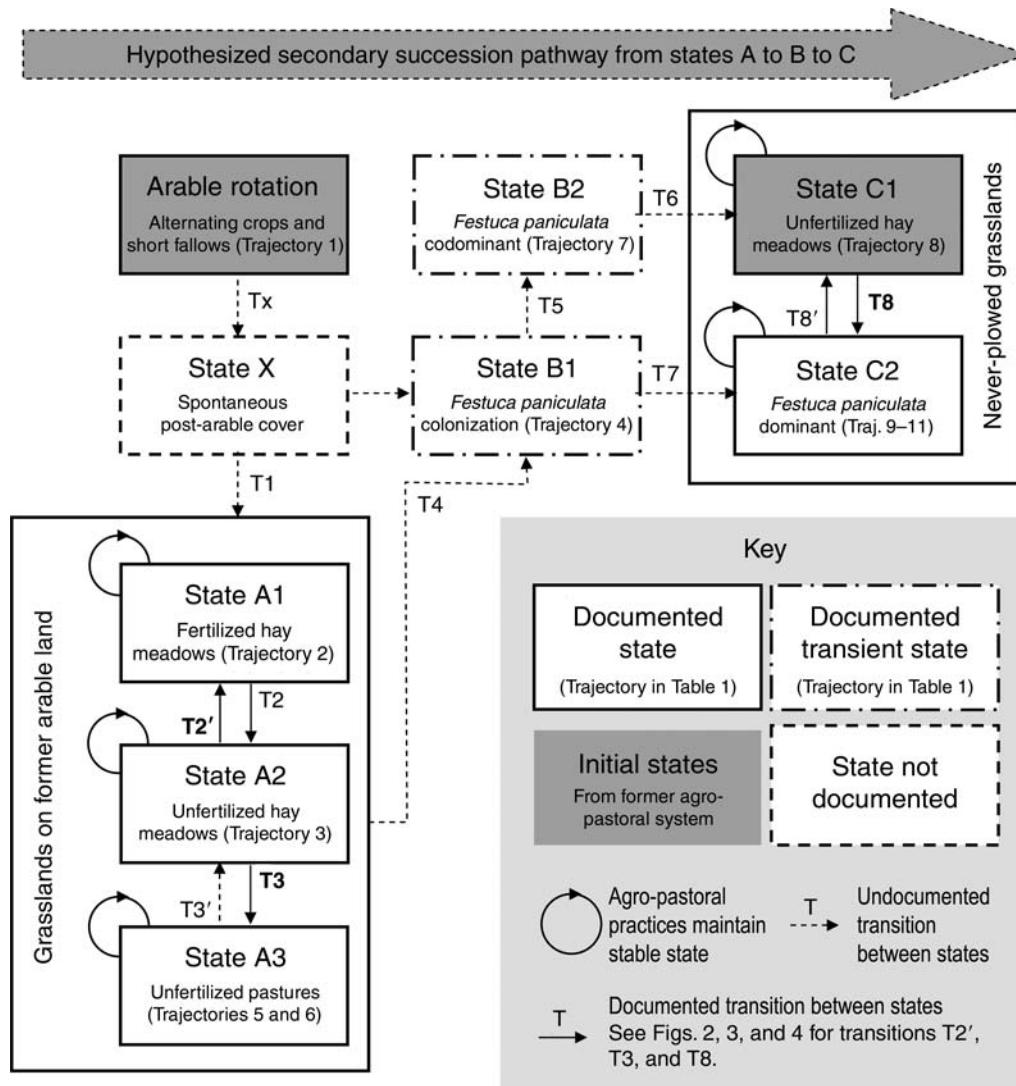
Fig. 1. Box and arrow representation of the state and transition model formulated for subalpine grasslands in Villar d'Arène, central French Alps. See Figs. 2, 3, and 4 for more details on transitions T2′, T3, and T8 (in boldface).

not used (trajectory 11 in Table 1; state C2 in Fig. 1). When no significant differences were found between trajectories in soil resources, disturbance regime, floristic composition, ecosystem properties, or plant traits (results not shown), they were pooled into common grassland states. Hence we merged trajectories 5 and 6 to form state A3, and trajectories 9, 10, and 11 to form state C2 (Table 1).

No recently converted arable fields were studied. No data is available on the short term colonization occurring after arable rotation ceased (undocumented transient state X; Fig. 1). Post-arable grasslands (states A1, A2, and A3; Fig. 1) were pooled into a block of states (A) within which we consider transitions to be reversible within a management time frame. Although no data is available on the duration of transitions T2 and T2′ local farmers told us that a few years of annual

fertilization (T2′) are enough to see changes in floristic composition and productivity of grasslands (Tasser and Tappeiner 2002). The reversibility of transition T3 is more uncertain as transition T3′ was not documented in our study.

States C form another block within which transitions are considered reversible. We documented transition T8 between state C1 and C2 following a change from hay cutting to grazing or abandonment (no agricultural use). Transition T8′ was documented in a similar site a few kilometers away (Bernard-Brunet et al. 1981, Jouglet and Dorée 1981, 1987, Bornard and Cozic 1986). It can be achieved using early cutting (before ear emergence of *Festuca paniculata*) or intensive grazing by cattle or horses (70 to 80 standard livestock units·d^{-1}·ha^{-1}; Jouglet and Dorée 1991).

TABLE 2. Significantly different environmental variables (direct effects: soil characteristics, nutrient availability, and disturbance regime) for each transition (Kruskall-Wallis test results) and the plant traits (indirect effects) they are sufficient to statistically "explain" when used as covariates in ANCOVA analysis of transition effect on plant traits.

Environmental variable	Kruskal-Wallis test (direct effects)				Plant traits	ANCOVA (indirect effects)				
	χ^2	P	N	Direction of change†		F	df	P	N	Direction of correlation‡
T2 (df = 1)										
NNI	3.857	0.05	6	−						
Soil pH	3.857	0.05	6	+	LCC	4.920	1, 2	0.113	6	−
Disturbance intensity§	3.857	0.05	6	−	LDMC	0.058	1, 2	0.825	6	−
					LCC	1.352	1, 2	0.329	6	+
					LNC	1.357	1, 2	0.328	6	+
					leaf toughness	0.839	1, 2	0.839	6	−
T3 (df = 1)										
Soil pH	5.400	0.020	9	+	LNC	3.492	1, 5	0.111	9	−
					LDMC	0.969	1, 2	0.398	6	+
					seed mass	2.101	1, 5	0.197	9	−
					leaf toughness	5.491	1, 2	0.101	6	+
Soil P (HF)	4.267	0.039	9	−	seed mass	1.471	1, 5	0.271	9	+
					LNC	3.457	1, 5	0.112	9	+
Disturbance date	3.857	0.050	9	−						
T8 (df = 1)										
Slope	4.225	0.040	12	+						
Soil pH	4.521	0.033	12	+						
Soil P (Olsen)	4.151	0.042	12	−						
Disturbance date	4.091	0.043	12	−	plant stature	1.446	1, 2	0.315	6	−
					LDMC	0.028	1, 2	0.877	6	+
Disturbance intensity¶	7.100	0.008	12	−	LDMC	1.405	1, 2	0.266	6	+
Transitions between states A, B, and C (df = 2)										
Elevation	19.768	<0.001	30	+						
Slope	9.767	0.008	30	+						
NNI	7.986	0.018	30	+						
KNI	16.574	<0.001	30	−	SLA	1.302	2, 24	0.289	30	+
Soil pH	17.045	<0.001	30	−	early-season ANPP	0.703	2, 9	0.418	15	−
Soil P (HF)	17.045	<0.001	30	−	SLA	0.132	2, 24	0.877	30	+
					LNC	1.195	2, 24	0.319	30	+
Soil P (Olsen)	9.970	0.007	30	−	SLA	1.056	2, 24	0.362	30	+

Notes: Key to abbreviations: NNI, nitrogen nutrition index; KNI, potassium nutrition index; LCC, leaf carbon content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; SLA, specific leaf area; ANPP, aboveground net primary productivity. Two measures of soil P were used: total P using the acid digestion method (HF; Olsen and Sommers 1982) and soluble phosphate using Olsen's procedure (Olsen et al. 1954).

† Direction of change between states.
‡ Direction of the correlation between the environmental variable and the plant trait.
§ Biomass loss (%).
¶ Height loss (%).

We propose that post arable grasslands where *Festuca paniculata* is present (trajectories 4 and 7) represent transient states in a post-arable colonization process by this species. This is illustrated in Fig. 1 as states B1 and B2 linking post-arable grasslands (state X) to states C (directly or via states A). In the following we explore the effects of this successional pathway by comparing blocks of states A, B, and C.

Land-use transition effects

Nutrient availability and disturbance regimes.—Table 2 summarizes the results of statistical analyses. The hypothetical successional gradient from blocks of states A to B to C was associated with increases in altitude and slope ($P < 0.001$ and $P = 0.008$ respectively, df = 2).

Concurrent strong gradients in soil properties were observed, with pH and both total and available P content decreasing while NNI increased (Table 2). No significant differences in disturbance regime were detected along the gradient. For transitions within blocks of states, steeper slopes in C2 compared to C1 were the only significant differences in topography, consistent with steeper slopes being more likely to be converted to grazing or abandoned.

Few differences in soil texture and no differences in soil water were associated with land-use transitions (Table 2). On the other hand significant differences in soil nutrients were detected. Nitrogen was assessed as limiting for plant growth in all grassland states (NNI below 80%) but nevertheless increased under regular

TABLE 3. Results of Kruskal-Wallis test for significantly different vegetation and ecosystem
  properties for each land-use transition.

Property	χ^2	P	N	Direction of change†
T2 (df = 1)				
Abundance of graminoids (%)	3.857	0.05	6	+
Abundance of tall leafy-stemmed dicots (%)	3.857	0.05	6	−
Abundance of anemochorous species (%)	3.857	0.05	6	−
Abundance of epizoochorous species (%)	3.857	0.05	6	+
Species density (no. contacts)	3.857	0.05	6	−
Maximum light interception (%)	3.857	0.05	6	−
Early-season SANPP	3.857	0.05	6	−
Early-season ANPP	3.857	0.05	6	−
Annual native litter mass loss (%)	3.857	0.05	6	−
Accumulated litter at snowmelt	3.857	0.05	6	+
T3 (df = 1)				
Annual standard litter mass loss (%)	3.857	0.05	6	+
Accumulated litter at snowmelt	3.857	0.05	6	+
T8 (df = 1)				
Abundance of graminoids (%)	4.521	0.03	12	+
Abundance of tall leafy-stemmed dicots (%)	4.521	0.03	12	−
Abundance of small leafy-stemmed dicots (%)	6.231	0.01	12	−
Abundance of small rosette dicots (%)	4.053	0.04	12	−
Abundance of anemochorous species (%)	4.861	0.03	12	−
Species density (no. contacts)	3.769	0.03	12	+
Early-season SANPP	3.857	0.05	6	−
Maximum standing biomass	3.857	0.05	6	+
Percentage living in maximum standing biomass	3.857	0.05	6	−
Overwinter native litter mass loss (%)	3.857	0.05	6	−
Accumulated litter at snowmelt	3.857	0.05	6	+
Transitions between states A, B, and C (df = 2)				
Plant biodiversity (Shannon index)	6.309	0.04	30	−
Plant biodiversity (Inverse Simpson's index)	7.563	0.02	30	−
Abundance of graminoids (%)	10.342	0.01	30	+
Abundance of legumes (%)	18.459	<0.001	30	−

Note: SANPP stands for specific aboveground net primary productivity.
  † Direction of change between states.

organic fertilization (from 58% to 70% under transition T2′; Table 2). However, organic fertilization did not appear to increase significantly the size of the soil N or P pools. Conversion to grazing was associated with a lower soil P (halved for transition T3, using Olsen's procedure). Significant increases in soil pH were also associated with decreases in the intensity of land-use such as cessation of fertilization (T2; from 6.8 to 7.3), and cessation of mowing in either formerly plowed (T3; from 7.3 to 7.7) or unplowed grasslands (T8; from 5.4 to 6.2; Table 2).

The proportion of aboveground biomass harvested by mowing increased by 66% following fertilization (T2′) compared to unfertilized fields (Table 2). On the other hand, conversion from mowing to light grazing (T3 and T8) induced more complex changes in disturbance regimes. Disturbance becomes selective and occurs earlier (T3, from 1006 to 418 degree days on average) with lower intensity (T8, from 84% to 19% height loss; Table 2).

Vegetation structure.—Plant diversity (both Shannon and Simpson's inverse index) decreased along the successional gradient across blocks of states A to B

and C, concurrent with an increase in the relative abundance of graminoids (including *Festuca paniculata*), and a decrease in legumes (Table 3).

No significant changes in species number or diversity were detected following fertilization (T2′) although a strong species turnover occurred. Six out of 13 dominant species (making up 80% of total abundance) were lost (e.g., *Briza media*, *Avenula pubescens*, *Helianthemum grandiflorum*, and *Sesleria caerulea*), whereas 13 species were gained (e.g., *Centaurea montana, Caerophyllum hirsutum, Gentiana lutea, Geranium sylvaticum, Heracleum sphondylium, Taraxacum officinale*). This strongly modified vegetation structure, with a decrease in the relative abundance of graminoids by 30% (especially stress-tolerant species such as *Bromus erectus* and *Sesleria caerulea*; results not shown) and up to a sixfold increase in large leafy stemmed dicots such as *Gentiana lutea* (Table 3).

Conversion to grazing on former arable fields (T3) had no significant effect on the relative abundance of morphological types (Table 3). However, palatable grass species such as *Dactylis glomerata* and *Trisetum flavescens* were lost from the 80% most abundant species

TABLE 4. Effects of different reproductive traits for each land-use transition

Reproductive trait	Transition 2 (df = 1)				Transition 3 (df = 1)				Transition 8 (df = 1)				Successive transitions between states A, B, and C (df = 2)			
	χ^2	P	N	Direc-tion	χ^2	P	N	Direc-tion	χ^2	P	N	Direc-tion	χ^2	P	N	Direc-tion
Anemochorous dispersal	3.857	0.050	6	−	3.267	0.071	9	+	4.861	0.027	12	−	7.852	0.020	30	−
Seed mass	2.333	0.127	6	+	4.267	0.039	9	−	0.214	0.644	12	−	8.640	0.013	30	

Note: "Direction" is the direction of change between states.

while less palatable grasses such as *Bromus erectus* and *Sesleria caerulea* became more dominant. Abandonment or conversion of C2 grasslands to light grazing (T8) also led to a substantial turnover of species. Conversion to sheep grazing (trajectory 10 of Table 1) led to a loss of half the dominant species (e.g., *Centaurea uniflora*, *Potentilla grandiflora*, *Trifolium alpinum*) that was not fully compensated by a gain of four species (e.g., *Bromus erectus*, *Daclylis glomerata*). Relative abundance of *Festuca paniculata* increased noticeably (but not significantly; $\chi^2 = 1.034$, $P = 0.309$, df = 1) to reach 61% driving an overall increase in the relative abundance of grasses (up 30%), while tall leafy dicots and small species decreased. Species loss and gain were even under conversion to cattle grazing (trajectory 9 of Table 1).

Ecosystem properties.—As vegetation density increased by 50% under fertilization (T2′), maximum light interception doubled reaching 70% (Table 3). ANPP and SANPP both increased (+30% for early season SANPP), resulting in a maximum standing aboveground biomass of 4.5 Mg/ha dry mass in fertilized hay meadows. Decomposition of native litter in these meadows was significantly faster than that of unfertilized meadows (A2), where average annual mass loss reached 33%. We observed less litter accumulated in spring in the fertilized A1 (0.5 Mg/ha dry mass) than in A2 grasslands (1.3 Mg/ha dry mass). No differences were detected for standard litter decomposition, indicating no significant changes in the decomposition environment.

Abandonment or conversion to grazing of C1 grasslands divided SANPP by 3. Maximum standing aboveground biomass doubled. It reached over 8 Mg/ha dry matter in C2 grasslands. Litter decomposition in C2 grasslands (25% annual litter mass loss) was 30% slower than in C1 grasslands where over 6 Mg/ha of litter was accumulated in the early spring (Table 3). Half of the peak standing biomass was senescent in C2 grasslands. As in the case of fertilization (transition T2′), no differences were detected in annual litter mass loss for standard litter ($\chi^2 = 0.429$, $P = 0.513$, df = 1).

Community-level plant traits.—Following Garnier et al. (2004), we compared the aggregated trait value across grassland states. Plant trait values reported in the text and in the Appendix refer to the community-aggregated trait values in each state or changes associated with various land-use transitions.

Anemochorous dispersal decreased significantly as seed mass increased from states A to C (Table 4). Comparing states A with states B and C, we detected an increase in LDMC indicating a shift from nutrient acquisition to nutrient conservation strategies (Table 5). LNC and SLA only responded marginally (Table 5). Leaf toughness is significantly higher in C states than in B states ($\chi^2 = 10.125$, $P = 0.001$, df = 1).

As hypothesized, fertilization (T2′) increased values for leaf traits such as SLA (up by one-third, reaching 18 m²/kg), LNC and LPC (Table 5). Leaf traits that are markers of leaf nutrient economy (Wright et al. 2004) were found to be correlated (e.g., LNC and LPC at $r = 0.94$, Pearson's $t = 10.1709$, $P > 0.0001$, df = 13), representing a syndrome of trait response to fertilization. LDMC and leaf toughness showed an expected opposite response, with leaves being six times tougher in A1 than in A2 grasslands (Table 5). Plant height increased by one-third following fertilization (Table 5), reaching an average of 26 cm.

Past land use (plowing) affected trait responses to conversions to grazing (Table 5). In never-plowed hay meadows (T8), plant height increased from 30 to 40 cm and significant changes were detected for leaf traits: LPC and LDMC decreased (Table 5). Leaf toughness did not increase significantly ($\chi^2 = 1.190$, $P = 0.275$, df = 1) but nevertheless reached its highest value in C2 grasslands (12 kg/cm tensile strength). *Festuca paniculata* is the dominant species in these grasslands and its leaves are over 50% tougher (17 kg/cm) than the second toughest leaves measured in this study (*Festuca nigrescens*, 11 kg/cm). When excluding *F. paniculata* from the calculation of community aggregated traits, LDMC and plant stature showed no response ($\chi^2 = 1.923$, $N = 12$, $P = 0.166$ and $\chi^2 = 0.419$, $N = 12$, $P = 0.518$, respectively). In the case of conversion to grazing on former arable fields (T3), leaf toughness increased by 50%. As expected, LNC and SLA decreased (−30% to 10 m²/kg; Table 5). Finally, seed mass decreased by over one-third when mowing ceased in previously plowed grasslands (T3; 0.3 g for 100 seeds in state A3; Table 4).

Linking nutrient availability and disturbance to ecosystem properties via plant traits

ANCOVA revealed that trait response to changes in nutrient availability were mediated by the intensity of light competition. We found that statistically, changes in

TABLE 5.   Significantly different plant traits for transitions and the ecosystem properties they are sufficient to statistically "explain" when used as covariates in ANCOVA analysis of transition effect on ecosystem properties (see legend of Table 2 for additional explanation).

| Environmental variable | Kruskal-Wallis test (direct effects) | | | | Plant traits |
	χ^2	P	N	Direction of change†	
T2 (df = 1)					
Plant stature	3.857	0.05	6	−	graminoid abundance (%) early-season ANPP maximum light interception accumulated litter at snowmelt
LCC	3.857	0.05	6	−	graminoid abundance (%) accumulated litter at snowmelt
LNC	3.857	0.05	6	−	early-season SANPP early-season ANPP accumulated litter at snowmelt
LPC	3.857	0.05	6	−	early-season SANPP early-season ANPP
SLA	3.857	0.05	6	−	early-season SANPP early-season ANPP
LDMC	3.857	0.05	6	+	graminoid abundance (%) early-season SANPP early-season ANPP accumulated litter at snowmelt
Leaf toughness	3.857	0.05	6	+	graminoid abundance (%) early-season ANPP accumulated litter at snowmelt
T3 (df = 1)					
LCC	3.851	0.05	6	+	
LNC	5.400	0.020	9	−	accumulated litter at snowmelt
LPC	3.857	0.05	6	−	accumulated litter at snowmelt
SLA	5.400	0.020	9	−	
LDMC	3.857	0.05	6	+	
leaf toughness	3.857	0.05	6	+	accumulated litter at snowmelt
T8 (df = 1)					
Plant stature	5.342	0.021	12	+	early-season ANPP maximum standing biomass litter decomposition rate
LPC	3.857	0.05	6	−	graminoid abundance (%) large-rosette dicot abundance (%) small leafy-stemmed dicot abundance (%) legume abundance (%)
LDMC	6.231	0.013	12	−	early-season SANPP maximum standing biomass accumulated litter at snowmelt litter decomposition rate
Transitions between states A, B, and C (df = 2)					
Plant stature	19.44	<0.001	30	+	legume abundance (%)
LCC	13.814	0.001	30	+	
LNC	5.948	0.051	30	−	
SLA	5.595	0.05	30	−	plant diversity§ plant diversity¶ graminoid abundance (%)
LDMC	8.449	0.015	30	+	

† Direction of change between states.
‡ Direction of the correlation between the plant trait and the environmental variable.
§ Inverse Simpson's index.
¶ Shannon index.

LNC under transition T2′ could be explained by increasing light interception ($F = 7.385$, df = 1, 2, $P = 0.073$; see Fig. 2). Under transition T3 on the other hand, some changes in leaf traits that are markers of leaf nutrient economy could be explained by changes in the soil. Lower LNC for example was statistically explained by a lower soil total P (Fig. 3, Table 2). No significant relationship was detected with LPC although LPC and

TABLE 5. Extended.

	ANCOVA (indirect effects)			
F	df	P	N	Direction of correlation[‡]
0.414	1, 2	0.566	6	−
0.414	1, 2	0.566	6	+
1.000	1, 2	0.391	6	+
1.228	1, 2	0.349	6	−
2.191	1, 2	0.235	6	−
6.069	1, 2	0.091	6	−
1.891	1, 2	0.263	6	+
0.211	1, 2	0.677	6	+
1.606	1, 2	0.294	6	−
0.473	1, 2	0.541	6	+
3.934	1, 2	0.142	6	+
0.427	1, 2	0.560	6	+
4.545	1, 2	0.123	6	+
3.391	1, 2	0.163	6	+
0.090	1, 2	0.784	6	−
0.550	1, 2	0.512	6	−
7.551	1, 2	0.071	6	+
0.121	1, 2	0.751	6	+
0.169	1, 2	0.709	6	−
2.142	1, 2	0.240	6	+
0.737	1, 2	0.454	6	−
0.853	1, 2	0.424	6	−
0.027	1, 2	0.879	6	+
0.075	1, 2	0.802	6	−
1.392	1, 2	0.323	6	+
0.239	1, 2	0.658	6	−
0.023	1, 2	0.888	6	−
3.839	1, 2	0.145	6	+
3.827	1, 2	0.145	6	+
0.093	1, 2	0.780	6	+
0.042	1, 2	0.850	6	+
2.945	1, 2	0.185	6	−
0.031	1, 2	0.871	6	−
0.363	1, 2	0.589	6	+
2.714	2, 24	0.085	30	−
1.884	2, 24	0.098	30	+
2.538	2, 24	0.098	30	+
2.864	2, 24	0.075	30	−

LNC are highly correlated across sampled field sites ($r = 0.94$, $P < 0.0001$).

The increase in the percentage of biomass harvested (a measure of disturbance intensity) following fertilization (T2′) explained changes in leaf traits (Table 2), but not the increase in plant height (the effect of T2′ is still significant in the ANCOVA; $F = 28.447$, df = 1, 2, $P = 0.013$). Changes in disturbance date or percentage of height loss (another measure of disturbance intensity) associated with the conversion of C1 grasslands from mowing to grazing or abandonment (T8) explained the increase in plant stature and the decrease in LDMC (Fig. 4, Table 2). However, in this case these changes in traits could also reflect the increase in abundance of *Festuca paniculata* (Fig. 4).

Changes in plant traits associated with land-use transitions were often sufficient to statistically explain changes in ecosystem properties (Table 5). Using stature as a covariable, ANCOVA results indicate that the abundance of taller plants explained the higher vegetation density ($F = 1.872$, df = 1, 2, $P = 0.265$) and increased light interception ($F = 1$, df = 1, 2, $P = 0.391$) following fertilization (Fig. 2). Likewise, increased early season SANPP in A1 relative to A2 grasslands could be explained by differences in the marker leaf traits of the plant nutrient economy spectrum (increasing SLA, LNC, LPC, and decreasing LDMC; Table 5). Changes in leaf toughness or LDMC explained changes in accumulated litter following fertilization (T2′, decrease) or conversion to grazing (T3 and T8, increase; Table 5). Increased LDMC also explained the lower litter decomposition rate in C1 as compared to C2 grasslands (T8; Table 5).

DISCUSSION

Within the proposed S and T model, we first tested a set of hypotheses on plant trait response to changing fertility and disturbance under complex land-use change. A second set of hypotheses concerned the ecosystem effects of changes in plant traits. We first return to these hypotheses and then discuss the insights gained from integrating plant-trait-based approaches to vegetation and ecosystem dynamics with the flexible S and T model approach.

Response of vegetation structure to fertility and disturbance via plant traits

By using the N, P, and K nutrition indices, we assessed the difference between the sward's nutritional requirements and what it finds in the soil, as calculated using the critical N curves described in *Methods*. We were able to detect increases in N availability (e.g., between blocks A, B, and C and following organic fertilization; T2′) without significant changes in the total soil N pool because not all soil N is available for plant growth.

As well as increasing nutrient availability, organic fertilization increased incoming light interception, which should result in increased competition for light. Successful plants outgrow their competitors through taller stature and faster growth rates (Goldberg and Landa 1991, Aerts 1999). Faster growth is achieved through increased SLA and LNC, and decreased LDMC (Chapin 1993, Poorter and Garnier 1999). Similar
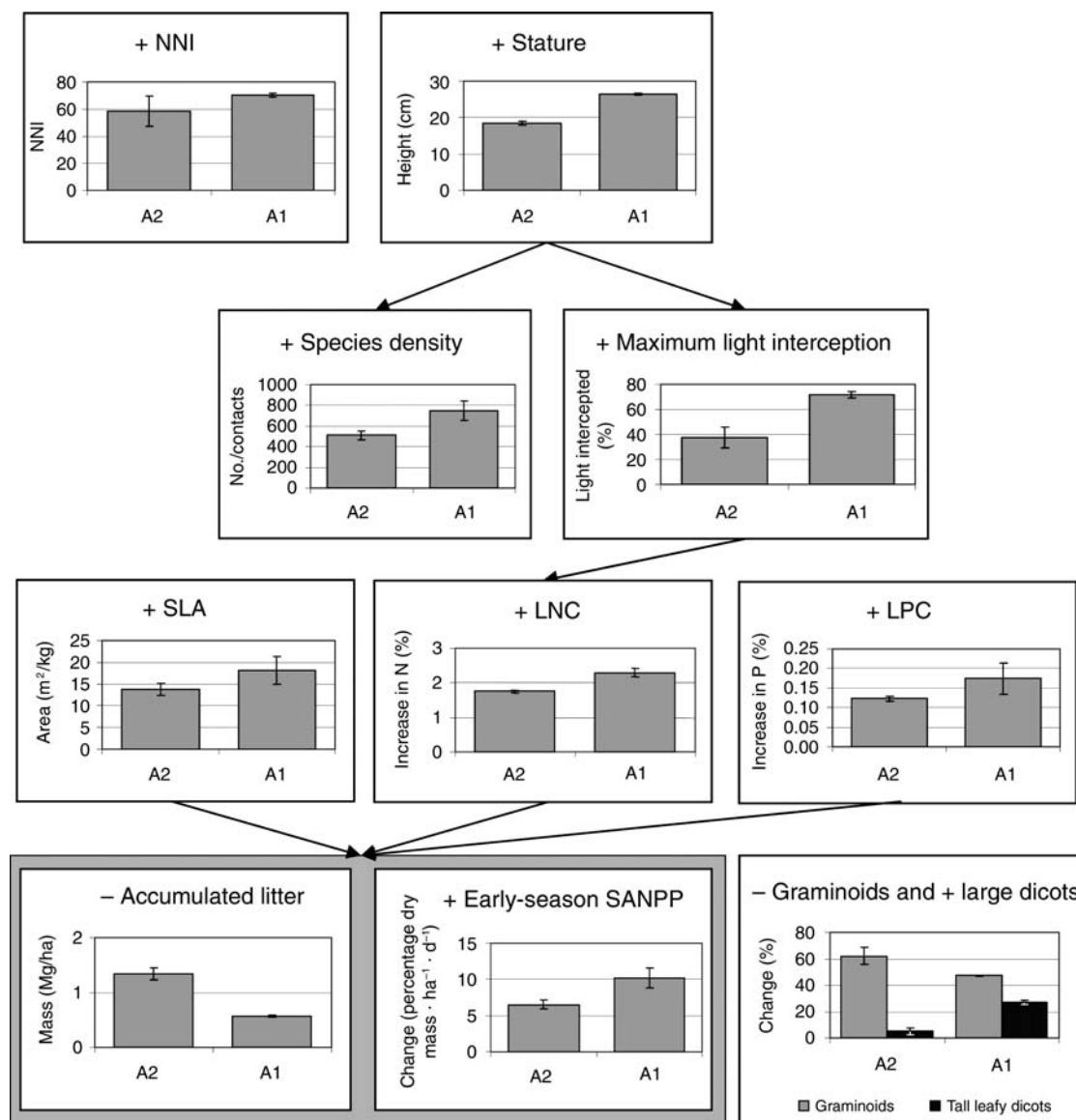
FIG. 2. Illustration of the significant effects of regular organic fertilization of previously unfertilized post-arable hay meadows (transition T2′ from states A2 to A1) on vegetation structure and ecosystem properties via plant traits. Arrows indicate significant ANCOVA results ($P < 0.05$) where the source changes in the input variable (e.g., maximum light interception) are sufficient to statistically explain the changes in the output variable (e.g., LNC). Abbreviations: NNI, nitrogen nutrition index; LNC, leaf nitrogen content; LPC, leaf phosphorus content; SLA, specific leaf area; SANPP, specific aboveground net primary productivity. Plus (+) and minus (−) signs indicate the direction of the variable's response to the land-use transition. Error bars show ±SE.

response patterns have been observed in other mountain grasslands, where fertilization was associated with a shift toward nutrient acquisition strategies (Bahn et al. 1999, Ansquer et al. 2004, Louault et al. 2005; S. Gaucherdand and S. Lavorel, *unpublished manuscript*). Within the plant community, species with traits promoting nutrient acquisition increased in abundance with regular fertilization. In our study, stress-tolerant graminoids (such as *Briza media* and *Sesleria caerulea*) were replaced by taller fast-growing dicots with leafy stems (such as *Centaurea montana*, *Caerophyllum hirsutum*, or

Geranium sylvaticum), resulting in a distinct grassland physionomy. Contrary to many observations in montane and subalpine pastures, however, fertilization did not result in a decrease in species number or diversity (Cernusca et al. 1996, Myklestad and Sætersdal 2004; see also Gough et al. 2000 for other vegetation types), probably because levels of nutrient availability remained relatively low even under regular organic fertilization (as indicated by NNI < 80%). Although we do not know what the exact amounts of fertilizer applications were in our field plots, locally, the highest fertilization rates
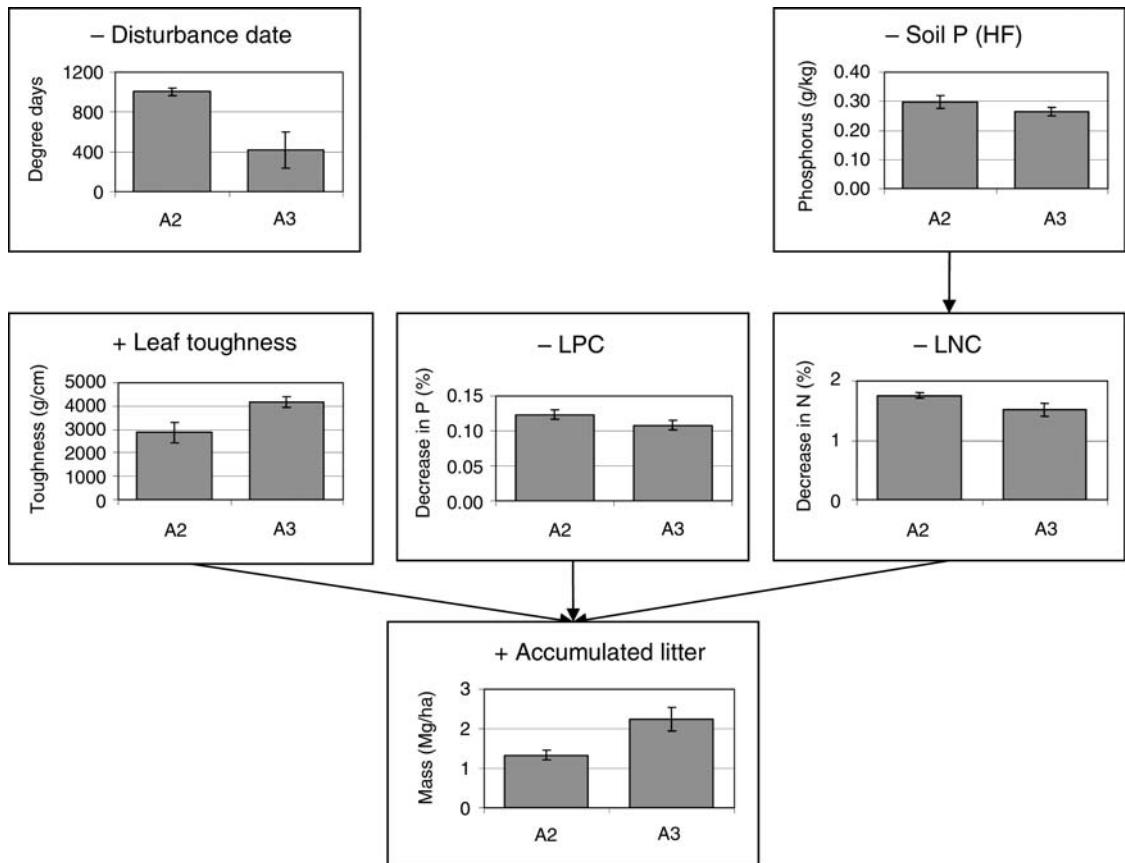
Fig. 3. Illustration of the significant effects of conversion of post-arable grasslands from hay cutting to grazing (transition T3, from states A2 to A3) on vegetation structure and ecosystem properties via plant traits. Arrows indicate significant ANCOVA results (refer to Fig. 2 for a brief explanation). Leaf toughness (protocol in Cornelissen et al. [2003]) is a measure of the weight necessary to tear a leaf of a particular width. Plus (+) and minus (−) signs indicate the direction of the variable's response to the land-use transition. Error bars show ±SE.

reach 40–50 Mg/ha of farmyard manure every five years (Picart and Fleury 1999).

In more nutrient-limiting situations, disturbance selectivity favors disturbance avoidance as indicated by the increase in leaf toughness (Díaz et al. 2001). Tussock architecture is an efficient way of avoiding grazing (Briske 1996), and tussock grasses such as *Bromus erectus* and *Festuca paniculata* are favored when hay meadows are converted to grazing (see Plate 1). This decreases the overall palatability of the grassland and, when given the choice, sheep and cattle only consume around 15% of the standing biomass (disturbance intensity in C2 grasslands). Such changes have been commonly observed in many grasslands of the world (Sternberg et al. 1999, Brzosko 2001; Díaz et al., *in press*), in particular in montane and subalpine meadows (Dorioz and van Oort 1991, Tappeiner and Cernusca 1993, Austrheim et al. 1999, Tasser et al. 1999, Barbaro et al. 2000, Fischer and Wipf 2002, Casals et al. 2004, Sebastià et al. 2004).

We found that past plowing favored plants with lighter, wind-dispersed seeds. This is consistent with our hypothesis that species with lighter, wind-dispersed

seeds will be more abundant in old fields recently (<50 years) converted to grasslands through spontaneous revegetation (Westoby et al. 1996, Tackenberg et al. 2003).

On never-plowed grasslands, both light grazing and abandonment lead from C1 to C2 grasslands. This suggests that, at our site, dense *Festuca paniculata* dominated grasslands may be an arrested successional stage (or para-climax [Connell and Slatyer 1977]), rather than moving toward colonization by dwarf shrubs as observed in many other subalpine grasslands after cessation of mowing or grazing (e.g., Pérez-Chacón Espino and Vabre 1987, Tappeiner and Cernusca 1993, Tasser and Tappeiner 2002). Similar pathways have been described under a diversity of other unproductive climatic and edaphic conditions, such as in lowland grasslands (e.g., Mitchley and Willems 1995, Kleijn 2003, Liancourt 2005), montane grasslands (e.g., Moog et al. 2002, Barbaro et al. 2000), Mediterranean old fields (e.g., Escarré et al. 1983), or temperate heathlands (e.g., Berendse et al. 1994).

Overall, our results validate our hypotheses on trait response to fertility and disturbance. By linking changes
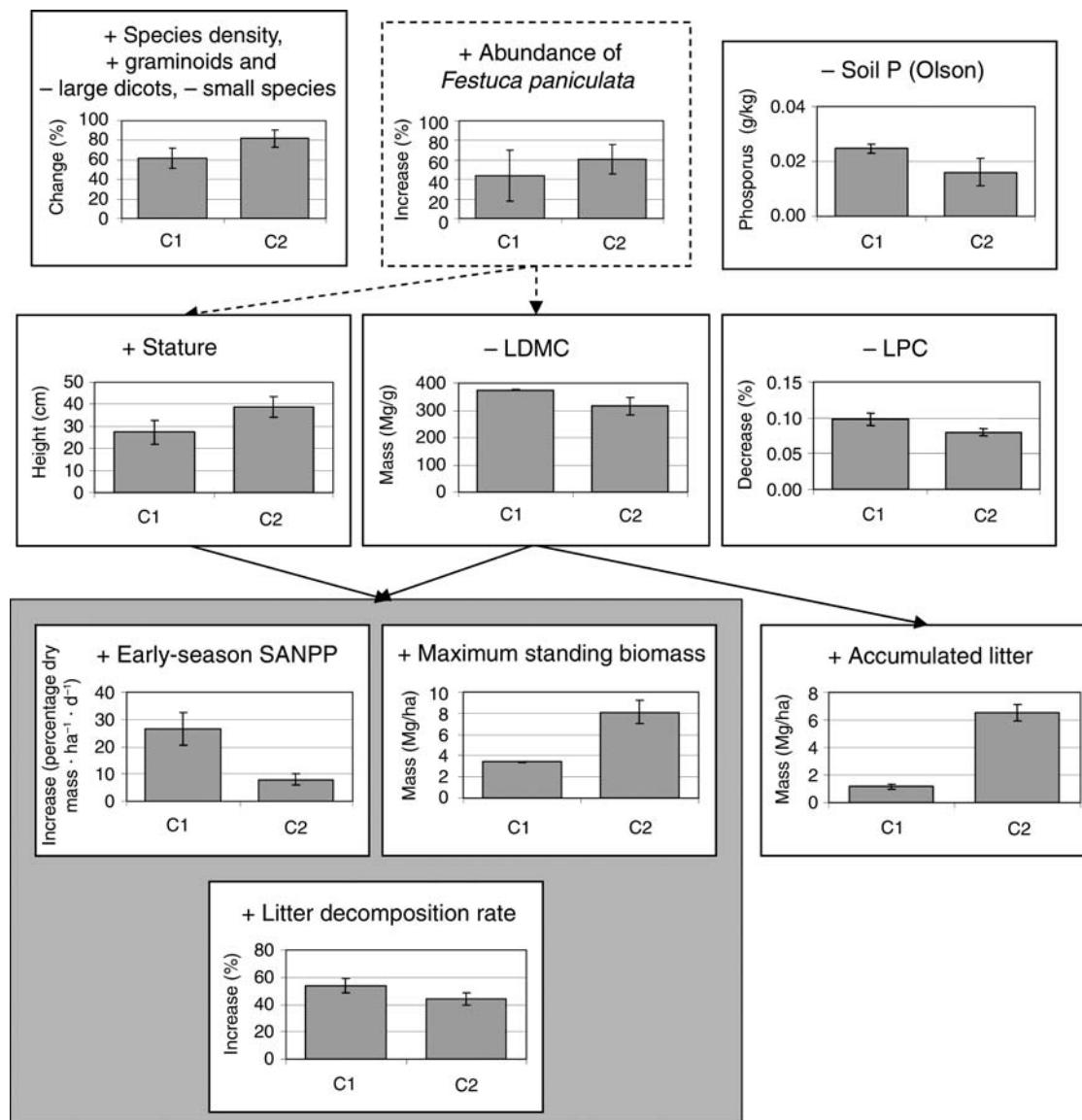
FIG. 4.   Illustration of the significant effects of conversion of never-plowed hay meadows to light grazing (transition T8 from states C1 to C2) on vegetation structure and ecosystem properties via plant traits. Arrows indicate significant ANCOVA results (refer to Fig. 2 for a brief explanation). The dashed box and arrows represent the fact that when the dominant tussock grass *Festuca paniculata* was excluded from the community-aggregated trait calculation, no significant differences were found in stature or leaf dry matter content (LDMC). Plus (+) and minus (−) signs indicate the direction of the variable's response to the land-use transition. Error bars show ±SE.

in fertility and disturbance to relevant leaf and plant traits, our results also show how plant traits can contribute to a process-based understanding of land-use change effects on vegetation structure.

Vegetation response to fertility and disturbance affects biogeochemistry via plant traits

Changes in plant traits in response to fertility and disturbance regimes appeared to directly translate to changes in ecosystem functioning, as a result of overlap between these traits and traits that govern biogeochemistry (Lavorel and Garnier 2002). Hence the shift in the

nutrient economy of the dominant plants from conservation to acquisition in response to regular fertilization accounted for the increase in specific net aboveground primary productivity. Similar effects were found for Mediterranean old field succession (Garnier et al. 2004). No difference was detected in the decomposition rate of standard litter, suggesting that lower LDMC accounted for faster leaf litter decomposition (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000, Garnier et al. 2004). This resulted in less accumulated litter. Similarly, more selective and less intense disturbance (conversion to grazing in T3 and T8) favored nutrient conservative

PLATE 1. *Festuca paniculata* tussocks stand out in a C2 grassland after it was recently grazed by sheep, Villar d'Arène, France. Photo credit: S. Lavorel.

species whose share of internal N recycling at senescence is higher. Such changes slow down the N cycle and lower leaf litter quality (Loiseau et al. 2005). Here, the increase in leaf toughness following conversion to grazing had an indirect effect on nutrient cycling through lower decomposability, leading to higher levels of litter accumulation.

The above changes are consistent with changes in marker leaf traits (e.g., LDMC, LNC) indicating faster individual growth rates (i.e., higher N uptake rates) and higher litter decomposition rates (i.e., higher N restitution rates; Garnier et al. 2004). Such changes may be related to direct responses of soil microbial communities to fertilization through N mineralization (e.g., Zeller et al. 2000) in addition to direct effects of changes in the quality of plant material (Güswell et al. 2005, Loiseau et al. 2005). Overall, these results strengthen the recently growing body of evidence for the role of plant traits in ecosystem functioning (Grime 2002, Lavorel and Garnier 2002, Chapin 2003; Lavorel et al., *in press*). The sets of correlational relationships highlighted by our analysis would need to be further explored using more sophisticated methods such as path analysis (Vile et al. 2006) in order to clarify causal chains between environmental variables, ecosystem properties and traits such as LNC and LPC.

By analyzing the effects of changing land-use and abiotic conditions on community-level plant traits and linking these quantitatively to changes in ecosystem properties, we showed that key traits associated with plant mineral resource economy are sufficient to explain basic biogeochemical processes such as above-ground primary productivity and litter dynamics (but see Eviner and Chapin [2003] regarding more complex processes). Our results thereby also support the biomass ratio hypothesis (Grime 1998), demonstrating that species effects on biogeochemistry may be directly proportional to their abundance (Garnier et al. 2004).

Long term land-use dynamics set the context for trait mediated vegetation and ecosystem response to current management

Our results show that the historical context of management decisions to cut or graze (T3 and T8) is important. Being set on higher and steeper slopes, grazed fields have probably received less organic fertilization during their long agricultural and pastoral history. As soil P is not very labile, this potentially explains higher soil P contents in grasslands that are still cut for hay in the current farming context. Similar land-use legacies involving long lasting effects of fertilization on soil P have been identified elsewhere in subalpine grasslands (e.g., Schütz et al. 2003) or forests (Dupouey et al. 2002, Fraterrigo et al. 2005). The decrease of soil P content from states A to B and C is consistent with this interpretation.

We also found an increase in N availability from states A to B to C. The higher NNI of A1 grasslands did not compensate for the low NNI of A2 and A3

grasslands as compared to the high NNI of both C1 and C2 grasslands. The detected decrease in pH from states A to B to C was consistent with other studies of secondary succession in highly constrained environments (e.g., Cernusca et al. 1996, Tasser et al. 1999). The observed increase in plant stature and seed mass, and the shift to nutrient conservation strategies from states A to B and C were also consistent with other studies investigating trait response during the herbaceous phases of secondary succession (Prach et al. 1997, Garnier et al. 2004, Kahmen and Poschlod 2004). Our results thus suggest that long-term successional dynamics (where response takes a few decades) interact with short-term changes in management (where response takes a few years) to explain the dynamics of vegetation and ecosystem properties in subalpine grasslands of Villar d'Arène (e.g., Cernusca et al. 1996, Austrheim and Olsson 1999).

In this study, the S and T approach has proven useful in integrating both of these time scales into a common operational framework. Their flexibility lies in that S and T models can be used as both heuristic and empirical tools. They are easy to modify to reflect evolving knowledge and have thereby proved useful in the development of hypotheses on ecological processes (Allen-Diaz and Bartolome 1998, Bestelmeyer et al. 2003, Briske et al. 2003, Herrick et al. 2006). Here, we successfully used an S and T framework to demonstrate how plant functional traits can be used as markers of processes occurring on both long and short time scales (Didham and Watts 2005), providing a mechanistic interpretation of vegetation and ecosystem responses to complex past and present land-use changes (Grime 2002, Briske et al. 2005).

Incorporating process-based understanding of vegetation and ecosystem dynamics into a state and transition framework using plant traits

As previously argued, rather than considering grasslands states A and C as alternative stable states resulting from past plowing, our results thus suggest considering them as successional stages. Grassland management decisions to cut or graze usually take into account a multiplicity of factors including ecosystem properties (productivity and palatability) and technical constraints (possibility of mechanized cutting on steep slopes). Local farmers, however, highlighted that, in Villar d'Arène, ecological feedbacks associated with management are secondary to the technical constraints of slope and elevation when deciding to use a field for hay harvesting or grazing. However, experimental research has shown that in the case of C2 grasslands (dominated by *Festuca paniculata*) the conversion back to species-rich meadows (C1 grasslands) requires very specific management actions such as early season mowing and grazing at a relatively high stocking rate (transition T8′ as documented in Jouglet and Dorée [1981, 1987, 1991]). These decisions are unlikely in the current economic context

(Quiblier and Senn 2004). As a result, C2 grasslands could be considered as the end point of all vegetation dynamics of subalpine grasslands in Villar d'Arène.

State and transition models were developed to accommodate possible alternative vegetation states (e.g., Allen-Diaz and Bartolome 1998; see also Jackson and Bartolome 2002 on non-equilibrium dynamics). Although we found that the effects of fertilization (transition T2′) on ecosystem properties (via plant traits; Fig. 2) are rapid, these effects may persist for many years. The cessation of fertilization (T2) could thus induce a slow trait and ecosystem response (e.g., Schütz et al. 2003). Also, dispersal limitations could slow the underlying successional dynamics described above (e.g., Fischer and Stöcklin 1997, Stampfli and Zeiter 1999) leading to transient states that can be considered as stable in a management time frame (e.g., Valone et al. 2002). In spite of the strong argument for considering that grassland states A, B, and C are stages in a predictable successional pathway to C2 grasslands, the S and T framework allows alternative stable states to remain as both a working hypothesis for further enquiry, and as a management tool for manipulating subalpine grasslands in Villar d'Arène.

In relation to the above considerations, our results also show that trait responses to changes from mowing to grazing differed on the basis of past plowing. In post-arable grasslands, we found an expected decrease in leaf nutrient concentration (LNC and LPC) while leaf toughness increased as grazing avoidance is favored (Figs. 3 and 4). On never-plowed grasslands, on the other hand, we observed a decrease in LDMC as plant height increases (Fig. 4). In the latter, trait responses were not significant when the dominant *Festuca paniculata* was excluded from the community aggregated trait calculation, indicating strong species-specific effects on the trait and ecosystem response to changes in management (Fig. 4). This underlies the possible keystone role *F. paniculata* plays in driving ecosystem dynamics in never plowed grasslands. Further understanding of these dynamics will require a more detailed understanding of this species' biology and ecology, and especially of its regeneration niche (Poschlod et al. 1998).

The S and T approach was developed in part to help frame ecosystem management within temporal variability in climate (e.g., Westoby et al. 1989, Milton and Hoffmann 1994). In this study, plant traits were useful in revealing that distinct dynamics operate in former arable fields and never plowed grasslands. These findings suggest that past plowing has a long term effects (land-use legacy) on ecological processes in subalpine grasslands. Land-use legacies can also—and indeed should—be incorporated into S and T based approaches to vegetation and ecosystem dynamics (e.g., Prober et al. 2002).

Conclusion

We successfully used a state and transition framework to demonstrate how plant functional traits can be used to

provide a mechanistic interpretation of vegetation and ecosystem responses to complex past and present land-use changes (Grime 2002, Briske et al. 2005). We show that resuming regular organic fertilization increases ecosystem efficiency (specific net aboveground primary productivity) and accelerates nutrient cycling by selecting taller plants with greater leaf nitrogen content through increased light competition. Conversion from indiscriminate cutting (for hay) to selective grazing leads to slower biogeochemical cycles. Unpalatable plants, with tough leaves or high leaf dry matter content, are favored, leading to high accumulations of standing dead biomass and litter. As functional markers (sensu Garnier et al. 2004) plant traits serve to link grassland response to management changes to their repercussion on ecosystem properties, on both the short time scale of current management alternatives (fertilization, cutting, grazing) and long term successional dynamics as they are affected by arable land-use legacies. We therefore conclude that plant traits provide a welcome addition to state and transition models when making projections or predictions of ecosystem response to management options.

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APPENDIX

Ecological variables describing each grassland state (*Ecological Archives* M077-002-A1).