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Plasticity of Plant Form and Function Sustains Productivity and Dominance along Environment and Competition Gradients. A Modeling Experiment with GEMINI

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1**Running title:** Plant plasticity modeling experiment

2**Title: Plasticity of plant form and function sustains productivity and dominance along**
3**environment and competition gradients. A modeling experiment with GEMINI.**

4Vincent Maire¹, Jean-François Soussana¹, Nicolas Gross^{1*}, Bruno Bachelet^{1**}, Loïc Pagès²,

5Raphaël Martin¹, Tanja Reinhold³, Christian Wirth^{3***} and David Hill^{4****}

6

7¹INRA UR874 UREP, Grassland Ecosystem Research, F-63100 Clermont-Ferrand, France

8²INRA UR1115 PSH, Plantes et Systèmes de cultures Horticoles, F-84914 Avignon, France

9³Max-Planck Institute for Biogeochemistry, D-07745 Jena, Germany

10⁴Clermont Université, Université Blaise Pascal, LIMOS, BP 10448, F-63000 Clermont-Ferrand,

11France

12* Current address: CNRS, Centre d'étude Biologique de Chizé, 79360 Beauvoir-Sur-Niort, France

13** Current address: Clermont Université, Université Blaise Pascal, LIMOS, BP 10448, F-63000

14Clermont-Ferrand, France

15*** Current address: Universität Leipzig, Institut für Biologie I, 04103 Leipzig, Germany

16**** Current address: CNRS, UMR 6158, LIMOS, F-63173 Aubière, France

17Authors for correspondence (phone +33 473 62 44 23; e-mail jfsoussana@clermont.inra.fr.)

18Email addresses: nicolas.gross@cebc.cnrs.fr, david.hill@univ-bpclermont.fr, bachelet@isima.fr,

19rmartin@clermont.inra.fr, cwirth@uni-leipzig.de

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21Website of GEMINI project: <https://www1.clermont.inra.fr/urep/modeles/gemini.htm>

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23**Key-Words:** Partitioning, growth, carbon, nitrogen, functional balance, coordination theory,

24biodiversity; grassland community

25 ABSTRACT

26 GEMINI, a mechanistic model linking plant functional traits, plant populations, community
27 dynamics, and ecosystem scale fluxes in grasslands has been reported in a companion paper
28 (Soussana et al., 2012). For monocultures and six species mixtures of perennial grass species,
29 this model has been successfully evaluated against experimental data of above-ground net
30 primary productivity (ANPP) and plant community structure across nitrogen and disturbance
31 (cutting frequency) gradients. The GEMINI model combines two categories of processes: i) C
32 and N fluxes, ii) morphogenesis and architecture of roots and shoots and demography of
33 clonal plant axes. These two process categories constrain the form and function of the
34 simulated clonal plants within plastic limits. We show here that the plasticity of the simulated
35 plant populations accounts for well-established empirical laws: i) root:shoot ratio, ii) self-
36 thinning, iii) critical shoot N content, and iv) role of plant traits (specific leaf area and plant
37 height) for population response to environmental gradients (nitrogen and disturbance).
38 Moreover, we show that model versions for which plasticity simulation has been partly or
39 fully suppressed have a reduced ANPP in monocultures and in binary mixtures and do not
40 capture anymore productivity and dominance changes across environmental gradients. We
41 conclude that, along environmental and competition gradients, the plasticity of plant form and
42 function is required to maintain the coordination of multiple resource capture and, hence, to
43 sustain productivity and dominance.

441. INTRODUCTION

45The outcome of biotic interactions is a dynamic process which entails ‘*the explicit inclusion*
46*of organismal trade-offs, of environmental constraints, and of the basic mechanisms of*
47*interspecific interactions*’ (Tilman, 1990) to be predictable. In a companion paper (Soussana
48et al., 2012), we present the GEMINI model (Grassland Ecosystem Model with INdividual
49centred Interactions), which couples within a common modeling framework: carbon, nitrogen
50and water cycles (*ecosystem scale*), plant population dynamics based on resource competition
51(*community scale*) and physiological and morphological plasticity of clonal plants
52(*organismal trade-offs*).

53 An individual-centred approach was used to develop this coupling across scales and,
54hence, to develop a dynamical structure-function-diversity model capable of simulating the
55dynamics of plant species within a community as well as the role of traits and their plasticity
56for ecosystem functioning (Soussana et al., 2012; Maire, 2009). GEMINI is an individual-
57centred model, rather than being individual-based, since it simulates average individuals
58within each plant population. Here we show that the details of physiological, morphological
59and demographic mechanisms allowing plant and population plasticity in the model are both
60necessary and sufficient (according to the parsimony principle) to simulate major trends in
61productivity and dominance across the perennial grass species studied.

62 The individual-based modeling approach offers the possibility to simulate the plastic
63adjustments of plant form and function in response to resource levels mediated by interactions
64with neighbors (Höglind et al., 2001; Yin and Schapendonk, 2004). Such plastic responses are
65shown to be mainly phenotypic (Grassein et al., 2010), species-specific and sometimes
66adaptive when they are correlated positively to changes in plant growth (Useche and Shipley,
672010a, 2010b; Pontes et al., 2010). Competition / facilitation biotic interactions are in part
68determined by these plastic responses of plants to resource levels (Grime, 1973; Tilman,

691984), which may enhance species coexistence and complementarity in plant communities
70(Soussana and Lafarge, 1998). For instance, Van Ruijven and Berendse (2003) have shown a
71reduction of leaf nitrogen content associated with higher plant nitrogen use efficiency when
72species grew at higher diversity level, enhancing the complementarity of nitrogen use and the
73functioning of grassland community. Therefore, mechanisms underpinning species plasticity
74are a prerequisite to explain species assembly rules in grassland communities and their
75consequences for ecosystem functioning (Grime and Mackey, 2002). Structure-function-
76diversity models like GEMINI can help in understanding the role of plasticity for the adaptation
77of plant populations to environmental gradients across species diversity levels.

78 Phenotypic plasticity is only adaptive if it is properly co-ordinated with environmental
79fluctuation (Sultan, 2004; De Jong, 2005), *i.e.* when a plant modifies its phenotype by an
80appropriate amount and at a certain speed in order to optimize growth and fitness (Useche et
81al., 2010a). This principle is applied in the GEMINI model (see the companion paper, Soussana
82et al., 2012 for full details) through a coordination of above and below-ground resource
83capture that ensures that no resource is in excess (Chapin, 1991) and through the coordination
84of morphogenesis and of assimilate supply. First, physiological plasticity to light and nitrogen
85levels is obtained by combining: i) the functional balance hypothesis (Davidson, 1969;
86Wilson, 1988), which assumes that partitioning of growth between shoots and roots tends to
87balance shoot photosynthesis and root N acquisition to ensure C and N homeostasis; ii) the
88photosynthesis coordination hypothesis (Chen et al., 1993, Maire et al., 2012), which assumes
89that partitioning between shoot structures and photosynthetic proteins maintains a leaf protein
90content co-limiting the dark (Rubisco activity) and light driven (RuBP regeneration) reactions
91of C₃ leaf photosynthesis. Second, morphological plasticity is obtained by assuming a
92potential morphogenesis which adjusts the emission, the elongation and the senescence of
93leaves and roots in function of daily temperature and photoperiod and of daily temperature

94and soil nitrogen concentration, respectively (Lemaire, 1999; Wu et al., 2004). Third, at the
95population scale, daily temperature and PAR (photosynthetically active radiation) fraction at
96the bottom of the canopy determine the plant axis ramification process (Neuteboom and
97Lantinga, 1989; Lafarge et al., 2005). Finally, plant growth is simulated as the minimum
98between supply (assimilate partitioning and reserves remobilization) and demand
99(morphogenesis and ramification) limited growth rates.

100 In this second paper, we focus on the role of physiological, morphological and
101population plasticity for species net primary productivity (an estimator of fitness for clonal
102plants) along resource (nitrogen), disturbance (cutting frequency) and competition (mixtures
103versus monocultures) gradients. We first evaluate the ability of the model to account for well-
104established empirical laws concerning: i) resource-based adjustments in root / shoot ratio, ii)
105self-thinning, iii) critical shoot N content, and iv) role of plant traits (specific leaf area and
106plant height) for responses to environmental gradients (nitrogen and disturbance). By
107comparing model versions of different complexity, we then test the following hypothesis:
108plant morphological (root and shoot morphology) and physiological (leaf N content, leaf
109photosynthesis) plasticity, as well as plant population (axis density) plasticity, are needed for
110maintaining population fitness (*i.e.* above-ground net primary productivity) across resource,
111disturbance and competition gradients.

112

1132. METHODS

1142.1. Model purpose

115The model is described following the ODD (Overview, Design concepts and Details) standard
116protocol proposed by Grimm et al. (2006) for individual-based and agent-based models in
117Soussana et al. (2012). A detailed list of all 132 equations, as well as the 187 variables and the

118100 default parameter values and their units is available (at
119www1.clermont.inra.fr/urep/modeles/gemini.htm) and will be send on request.

120 The main purpose of GEMINI is to understand the dynamics and plasticity of plant species
121within a community and the role of traits and their plasticity for ecosystem functioning. The
122model considers climatic (short-wave radiation, temperature and precipitation) and
123atmospheric (CO₂ concentration) abiotic drivers. Management conditions concern both
124disturbance (through defoliation) and fertilization (inorganic and organic N supply). The
125model was built with a modular architecture, which allows the inclusion, or not, of a range of
126biotic agents (plant species, soil microbial decomposers and domestic herbivores) as well as
127environment and management modules (soil, vegetation, fertilization and cutting).

128 GEMINI can simulate a potentially unlimited number of plant species (or plant populations
129from the same species) from currently two plant functional types (perennial grasses and
130legumes). The model focuses on the acquisition and the utilization of two major resources
131(light and nitrogen) by plants and their consequences for the carbon and nitrogen cycles.

132

1332.2. State variables and scales

134GEMINI consists of vegetation, soil and herbivore sub-models, coupled with environment and
135management sub-models (for a full description of the model, see Soussana et al., 2012). The
136vegetation sub-model, named CANOPT is an individual-centred model of a multi-species stand
137comprising clonal grasses and/or legumes and forming a multi-layer plant canopy. Each
138clonal plant population is described as a collection of identical axes (*e.g.* tillers for grasses).
139Moreover, all plant species are assumed to be perfectly mixed in the horizontal plane. Plant
140population demography is calculated from the vegetative multiplication and mortality of axes.
141Other demographic processes, including flowering, fruiting, dispersion, germination and
142recruitment from seeds are not considered, since these processes are minimized by regular

143disturbance through cutting and grazing in temperate grasslands dominated by perennial
144clonal pasture species (*e.g.* Harper, 1978).

145 The vegetation sub-model consists of four modules: i) a biochemical module, which
146simulates the C and N balance and the partitioning of growth among shoot structures (W_S),
147leaf proteins (W_P) and roots (W_R) for mean plant axes in each plant population. For each plant
148population, the corresponding state variables are the axes number (D , m^{-2}), and the mass per
149axis of three structural compartments (W_S , W_P and W_R) and of C and N substrates and of two C
150and two N reserve compartments; ii) a shoot morphogenesis module, which computes the
151demography and size of leaves (two state variables, length and mass per leaf); iii) a root
152morphogenesis module, which computes the demography and size of roots (two state
153variables, length and mass per root); iv) a competition module which calculates short-wave
154radiation and inorganic N partitioning among mixed plant populations.

155 The environment sub-model calculates the microclimate within the canopy and the
156inorganic N balance of the soil (or of the substrate when the vegetation model is not coupled
157to the soil model). The management sub-model schedules events caused by grassland
158management (cutting dates, grazing periods, N fertilizer applications).

159

1602.3. Model parameterization and evaluation

161The experimental site used for model calibration was established in spring 2002 in an upland
162area of central France (Theix, 45°43'N, 03°01'E, 870 m a.s.l.) on a granitic brown soil
163(Cambisol, FAO). The local climate is semi-continental, with a mean annual temperature of
1649°C and a mean annual rainfall of 760 mm. 13 native perennial C_3 grass species that co-occur
165in mesic permanent grasslands were studied in monocultures: *Alopecurus pratensis*,
166*Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Elytrigia repens*,
167*Festuca arundinacea*, *Festuca rubra*, *Holcus lanatus*, *Lolium perenne*, *Phleum pratense*, *Poa*

168 *pratensis*, *Poa trivialis*, *Trisetum flavescens*. A *Lolium perenne* cultivar ('Clerpin') was added
169 as a control. Henceforth, species are referred to by their species (*e.g.* *A. pratensis*) name.

170 The calibration procedure of the model has been reported by Soussana et al., (2012).
171 Briefly, out of a total of 100 parameters, 65 have been considered as constant across the grass
172 species investigated with a value taken from the literature. The remaining parameters were
173 estimated by species from plant trait values measured in a non-limiting nutrient treatment
174 (360 kgN ha⁻¹ yr⁻¹; 3 cuts yr⁻¹) of the field experiment comparing 13 grass species grown in
175 monocultures (see the calibration of these parameters in Soussana et al., 2012). In this
176 treatment, neither nutrients nor water resources were limiting above-ground grass growth
177 (Pontes et al., 2007, Maire et al., 2009).

178 Two parameters (LL_{plast} , the branching order dependency of potential root length and
179 Tr , the thermal time interval between two successive root emission events) were optimized by
180 maximizing axis biomass (W_G). This first optimization was done on C-N+ management
181 treatment using constant axis density for each species. The two population demography
182 parameters ($intcl$, the clonal integration and $Tsen_0$, the lifespan of an axis) were then
183 optimized by fitting simulated to measured tiller density (D) per unit ground area. This second
184 optimization was done after the root parameters optimization.

185 Predicted and measured annual dry-matter yields were highly correlated without bias
186 across species, N supply and cutting frequency treatments in monocultures and in mixtures of
187 six species (Soussana et al., 2012). The GEMINI model could therefore simulate without bias
188 responses to nitrogen and disturbance gradients of net primary productivity and of plant
189 community structure.

190

191

192

1932.4. Experimental design for testing the model against empirical laws

194 We have tested model patterns against four types of well-established empirical laws: i)
 195 changes in root:shoot ratio following an abrupt change in resource availability, ii) self-
 196 thinning, iii) critical shoot N content decline during shoot growth, and iv) role of plant traits
 197 (specific leaf area and plant height) for population response to environmental gradients
 198 (nitrogen and disturbance). These patterns were studied with monocultures grown under
 199 constant environmental conditions ($T_a = 14^\circ\text{C}$, $PPFD = 700 \mu\text{mol m}^{-2} \text{s}^{-1}$).

200 First, short-term responses of model compartments to disturbance (cutting) and to
 201 nutrients stress (N deprivation) were tested. Two partitioning functions P and Q control the
 202 partitioning of dry matter between shoot and root structures and between shoot structures and
 203 shoot proteins, respectively. P is calculated as the functional balance between shoot C and
 204 root N capture rates (Eq. 1, adapted from Hilbert and Reynolds, 1991; see supplementary
 205 materials SI1 and SI2 in Soussana et al. (2012) for full details). Q is calculated following the
 206 coordination hypothesis of leaf photosynthesis (Chen et al., 1993; Maire et al., 2009).

$$207 P = \frac{f_C}{f_N} \frac{\sigma_{r_act} W_R l_{wr} f_{active_root}}{\sigma_C LA} \quad (\text{Eq. 1})$$

$$208 Q = \frac{f_{np} W_p D}{\sum_{z=1}^m N_{pac_z} LAI_z} \quad (\text{Eq. 2})$$

209 Where f_C / f_N is the C:N plant ratio, σ_{r_act} is the root N uptake rate, W_R is the root dry mass,
 210 l_{wr} is the root area to mass ratio, f_{active_root} is the proportion of active roots, σ_C is the net
 211 photosynthesis rate, LA is the plant axis leaf area, f_{np} is the N fraction in shoot proteins, W_p is
 212 the shoot proteins mass, D is the axis density per unit ground area, N_{pac_z} and LAI_z are the
 213 coordinated leaf photosynthetic content and the leaf area index in layer z , respectively. Power
 214 coefficients q_1 and q_2 vary the degree of control on partitioning for P and Q variables,
 215 respectively.

216 A critical N concentration curve is defined as being the minimum plant N
217 concentration allowing maximum growth rate and is related to stand dry matter accumulation
218 by a negative power function in a number of C₃ species, including perennial forage grasses
219 (Lemaire et al., 2008). The ability of the model to simulate critical shoot N content decline
220 during canopy regrowth was tested by simulating *D. glomerata* monocultures grown under
221 close to non-limiting nitrogen conditions (corresponding to the C-N+ experimental treatment).

222 Third, the model's ability to simulate self-thinning (*i.e.* the negative power law
223 relating the individual mass and the density of population units; *e.g.* Harper, 1978) was tested
224 across species in monocultures and for two N fertilizer supplies (N-, N+) at low cutting
225 frequency (three cuts per year).

226 Finally, the ability of the model to reproduce species specific responses to disturbance
227 and to nitrogen was tested for a range of measured plant functional trait values (*SLA*, specific
228 leaf area and plant height) by using simulated log response ratios (LNRR). Log response
229 ratios are the logarithms of the ratios of species performances along an environmental
230 gradient (Suding, et al., 2003), here at low vs. high cutting frequency (from 3 to 6 cuts yr⁻¹)
231 and at low vs. high N supply (from 12 to 36 g N m⁻² yr⁻¹). A positive LNRR value indicates a
232 higher species performance at the higher end of the gradient (*i.e.* at high cutting frequency and
233 at high N). Conversely, a negative value indicates a lower species performance at the lower
234 end of the gradient.

235

236 2.5. Testing the role of plant and population plasticity

237 To test the role of plasticity for net primary productivity and its stability along resource and
238 disturbance gradients (see Fig. 1 for the conceptual design of the modeling experiment), the
239 full GEMINI model (FP) was compared with simplified versions offering reduced plasticity
240 (from RP₁ to RP₄) and reduced coordination of growth (RP₅ and RP₆):

241- RP₁, full model but without axis demography resulting in constant axis density,
242- RP₂, same as RP₁ but without explicit root morphogenesis,
243- RP₃, same as RP₁ but without explicit shoot morphogenesis,
244- RP₄, same as RP₁ but without explicit root and shoot morphogenesis,
245- RP₅, same as RP₄ but with equal distribution of assimilates to leaf structure and leaf proteins,
246- RP₆, same as RP₄ but with equal distribution of assimilates to leaf structure and roots.
247 The corresponding modules (*i.e.* axis demography, root and shoot morphogenesis,
248assimilate partitioning) were inactivated either by setting parameter values to zero, or by
249replacing them by fixed parameter values (Table 1).

250 In order to suppress axis demography in RP₁, *intcl* and *Tsen₀* parameters were set to zero
251in the ramification module. In RP₂, RP₃ and RP₄, morphogenesis modules were replaced by
252constant parameter values by species (Fig. 1). In RP₂ and RP₄, root morphogenesis was
253replaced by two species-specific parameters: a constant area to mass ratio of roots (*lwr*) and a
254constant root senescence rate (*TRoot_{sen}*). In RP₃ and RP₄, shoot morphogenesis was replaced
255by a constant leaf area ratio (*LAR*, leaf area to plant mass ratio) and by a constant shoot
256senescence rate (*TShoot_{sen}*). In addition, the shoot architecture module was replaced by a
257constant plant canopy density (leaf area per unit canopy volume, *C_H*) and by a constant leaf
258angle (*theta*) (Table 1). In RP₅ and RP₆, fixed and equal assimilate fractions to leaf structure
259and leaf proteins (RP₅) and to leaf structure and roots (RP₆) were obtained by setting the value
260of *q₂* and *q₁* parameter to zero in Eq. 2 and 1, respectively.

261 The optimization procedure used for the full plasticity version (FP) was then applied to
262each reduced plasticity model version. In the reduced plasticity version RP₁, the two root
263parameters *LL_{plast}* (branching order dependency of potential root length) and *Tr* (thermal time
264interval between two successive root emission events) were optimized as in FP version.

265 Values of these parameters were calculated for each species using the outputs of previous
266 equilibrium simulations for the C-N+ treatment (Table 1B).

267 Reduced and full plasticity model versions were first compared for monocultures. Three
268 grass species, which are representative of three plant N strategies (Maire et al., 2009), were
269 used: *A. odoratum* (short and exploitative grass), *A. elatius* (tall and exploitative grass), and
270 *F. arundinacea* (tall and conservative grass). Then, in order to test the role of plasticity for the
271 outcome of plant-plant interactions, model versions with full and reduced plasticity were
272 compared with binary mixtures. Finally, simulated species and model versions were compared
273 along resource and disturbance gradients: (i) a light gradient with 100, 80 and 60 % of the
274 daily short-wave radiation (*PPFD*) of the experimental site; (ii) a nitrogen gradient
275 contrasting fertilization supply rates of 360, 120 and 60 kgN ha⁻¹ yr⁻¹; (iii) a disturbance
276 gradient with 8, 6, 3 and 1 cuts yr⁻¹.

277 Simulations were run for 10 years with the experimental site climate (years 2003-2004 in
278 loop for which data were available, see Pontes et al., 2007) and management conditions. Spin-
279 up runs and a restart procedure allowed initializing plant populations close to steady-state.
280 Simulations were stopped for a given plant population whenever the substrate C mass tended
281 towards zero (*i.e.* population death) or increased above an unrealistic value (greater than the
282 plant structural C mass). Means were calculated over the simulation period of the plant
283 population. With the FP model version simulations lasted in monocultures and mixtures 3655
284 and 3000 days, on average. With the RP₁ model version simulations lasted in monocultures
285 and mixtures 2237 and 1715 days, on average. Within three species mixtures, the average
286 duration of coexistence between two simulated species reached 473 days. Therefore, some of
287 the simulations lasted for a shorter time period than 10 years.

288

289

2902.6. Data analysis

291 An analysis of variance and Tukey's post-ANOVA comparisons at a p-level of 5% were used
292 to analyze simulated above-ground net primary productivity (ANPP) across species, plasticity
293 levels and environmental gradients in both monocultures and mixtures. Moreover, these tests
294 were also applied to model outputs indicating light and nitrogen capture: the absorbed fraction
295 of photosynthetically active radiation (*FAPAR*) and the nitrogen uptake rate per unit root area
296 (*Su*). All statistical tests were performed with the software - Statgraphics Plus (Manugistics,
297 Rockville, MD, USA).

298

2993. RESULTS

3003.1. Simulating co-limitation of growth by light and inorganic N capture

301 After a cut, the *P* partitioning variable peaks at a high value thereby increasing partitioning to
302 shoot structures at the expense of partitioning to root structures. During shoot regrowth after
303 cutting, the gradual increase in photosynthesis leads to an exponential decline in *P* which
304 tends asymptotically to one (Fig. 2A). This indicates the reestablishment of a functional
305 balance between roots and shoots. Cutting also induces a sharp drop in the second partitioning
306 variable (*Q*) as the residual leaf area becomes exposed to full radiation. This increases the leaf
307 N content required for photosynthetic coordination, leading to an increased partitioning to leaf
308 photosynthetic proteins at the expense of leaf structures. During shoot regrowth,
309 photosynthetic proteins replenishment increases asymptotically *Q* value towards one and leaf
310 photosynthesis coordination is re-established. Within one month after a cut, as *P* and *Q* values
311 both converge towards one, growth is again co-limited by nitrogen, light and CO₂ capture.

312 In the same way, after nitrogen deprivation a reduced root inorganic N uptake leads to a
313 decline in *P* value (Fig. 2B) and, thereby, to a preferential partitioning of assimilates to roots
314 compared to shoot structures. Both increased root growth and a de-repression of root N uptake

315capacity (Soussana et al., 2012) lead to a restoration of N uptake and to an asymptotic
316increase of P value towards one. Q is little affected by inorganic N deprivation (Fig. 2B) and
317its value stays close to one. Hence, by adjusting their root:shoot ratio and their N uptake
318capacity, N deprived plants tend towards a co-limitation of growth by nitrogen uptake and by
319photosynthesis. P and Q values show oscillations over a few days (Fig. 2). Such oscillations
320are caused by the emission and senescence of individual leaves and roots, which alters
321root:shoot functional balance through small changes in leaf and root area.

322

3233.2. Critical shoot nitrogen content decline

324Critical shoot N content (see Methods) declines with above-ground biomass (Lemaire et al.,
3252008) according to a power law. This empirical law was tested with *Dactylis glomerata* under
326close to non-limiting nitrogen conditions (corresponding to the C-N+ experimental treatment).
327During the first part of the regrowth, simulated shoot N concentration fits to the empirical law
328(Fig. 3), showing that this law may therefore be a consequence of coordinated plant growth.
329However, above a leaf area index of 5 simulated changes in shoot N content slightly
330underestimate the empirically established critical nitrogen decline curve.

331

3323.3. Simulating size vs. density relationships

333Between species variations in mean individual shoot mass (W_S+W_P) and mean density (D) of
334plant axes were negatively correlated according to a power law (exponent -0.94, Fig. 4A).
335Data obtained in spring in the field experiment (Maire, 2009) showed a similar exponent (-
3361.12) between mean shoot tiller mass and tiller density (Fig. 4B). Simulations of size vs.
337density relationships with both shoots and roots (Fig. 4A, W_G) indicated a lower exponent in
338absolute value (close to $-\frac{3}{4}$) of the size vs. density relationship. Therefore, the model captures
339an essential property of plant canopies that relates the size and density of a plant population.

3403.4. Predicted productivity vs. traits relationships.

341The simulated log-response ratio (LNRR) of above-ground net primary productivity (*ANPP*)
342to cutting frequency is significantly and positively correlated with *SLA* ($r^2 = 0.59$, $p < 0.01$,
343Fig. 5A). This indicates that the higher the *SLA* of the species, the higher its biomass at high
344compared to low cutting frequency. In the same way, the LNRR of *ANPP* to N supply is
345significantly and negatively correlated with plant height ($r^2 = 0.36$, $p < 0.05$, Fig. 5B). Hence,
346the lower the plant height, the higher its biomass at high compared to low N supply. Overall,
347these two results indicate that simulated species response to cutting frequency and N
348fertilization varies with plant functional traits and therefore with the functional strategy of
349species.

350

3513.5. Plant plasticity and simulated above-ground productivity in monocultures

352The role of plasticity for *ANPP* and its stability along cutting frequency, N supply and light
353gradients was tested with three grass species that are representative of contrasting N strategies
354(Maire et al., 2009) (Fig. 6, Table 2A). The full model (FP) provided a higher *ANPP* (Tukey's
355post-ANOVA comparison of multiple means, $p < 0.05$) than other model versions that
356restricted plasticity and coordination (Fig. 6). An intermediate *ANPP* was obtained for model
357versions without tiller dynamics and/or root, shoot morphogenesis (RP_1 , RP_2 , RP_3 and RP_4
358versions). Model versions which, moreover, suppressed coordination between shoot structures
359and roots, or between shoot structures and leaf proteins (RP_5 and RP_6) had significantly lower
360*ANPP* (Tukey, $p < 0.05$) than other versions. The large role of plasticity for *ANPP* was
361underlined by a 51 % share of total variance for this factor and its interactions with others.

362 Radiation and nitrogen captures (*FAPAR* and S_u , respectively) also varied strongly with
363plasticity level (42 and 32 % of total variance, Table 2A). An explicit root morphogenesis
364(RP_1 , RP_2 and RP_4) significantly increased root uptake activity (S_u) compared to model

365versions without root morphogenesis and architecture (Tukey, $p < 0.05$, data not shown). An
366explicit shoot morphogenesis (FP, RP₁ and RP₂ versions) increased the absorbed radiation
367(*FAPAR*) compared to intermediate plasticity (RP₃ and RP₄) (data not shown).

368 With full plasticity (FP), the three grass species showed contrasting behaviors in response
369to environmental gradients. *ANPP* responses to N fertilization indicated a strong increase for
370all species, except *F. arundinacea* which reached a plateau (Fig. 6). *ANPP* responses to
371cutting frequency were smaller than with N supply and displayed contrasted slopes among
372species (see FP Fig. 6). *F. arundinacea* reached its optimum *ANPP* around 3 cuts per year; *A.*
373*elatius* around 6 cuts yr⁻¹ and *A. odoratum* between 6 and 8 cuts yr⁻¹ (Fig. 6). *F. arundinacea*
374*ANPP* decreased strongly with increasing shade, while the two other species were less
375affected (Fig. 6). In contrast to the full model version (FP), there was almost no increase in
376*ANPP* for the least plastic versions (RP₅ and RP₆) when light and N supply levels were
377increased and when disturbance level was reduced (Fig. 6).

378

3793.6. Plasticity, productivity and dominance in binary mixtures

380Within binary mixtures, the fraction of total variance (12, 24 and 33% for *ANPP*, *FAPAR* and
381*S_u*, respectively, Table 2B) attributed to the plasticity level was relatively smaller than in
382monocultures. However, the plasticity x species interaction explained also a substantial share
383of the total variance (17 and 39%, respectively) of *ANPP* and of *FAPAR*. The decline in
384*ANPP* at reduced plasticity levels was not systematically observed in mixtures. However,
385*ANPP* was always low when growth partitioning coordination was suppressed (RP₅, RP₆, Fig.
3867).

387 In simulated binary mixtures, the dominance of *F. arundinacea* markedly declined with
388cutting frequency (Fig. 7). At three cuts per year, this tall grass overcompeted simulated *A.*
389*odoratum* and *A. elatius*, which were conversely dominant at higher cutting frequencies (Fig.

3907). This disturbance induced change in dominance became less marked when root and shoot
391morphogenesis were not modeled explicitly (RP₁ and RP₂) and was suppressed when growth
392partitioning coordination was knocked out (RP₅ and RP₆). In the latter case, the ANPP of
393simulated *F. arundinacea* was always close to zero (Fig. 7).

394 Within simulated mixtures of *A. odoratum* and *A. elatius*, *A. elatius* became increasingly
395dominant at high compared to low frequency when full plasticity was included. In contrast,
396when explicit root and shoot morphologies were suppressed (RP₂, RP₃ and RP₄), *A. odoratum*
397was favored by an increased cutting frequency (Fig. 7). Therefore, the outcome of simulated
398biotic interactions depended upon model assumptions on the degree of plant plasticity.

399

4004. DISCUSSION

401By combining an individual-centred approach with coordination hypotheses, we have
402developed a mechanistic model linking plant functional traits, plant population and plant
403community dynamics and ecosystem processes (*e.g.* net primary productivity). In agreement
404with our initial hypothesis, we have shown through a modeling experiment that both
405individual plant plasticity and population plasticity are needed to maintain grass species
406fitness (*i.e.* above-ground net primary productivity) along gradients of resource levels
407(nitrogen, light), disturbance (cutting frequency) and competition (mixtures vs.
408monocultures). Moreover, emergent properties arising from the model with full plasticity
409account for four well-established empirical laws: i) resilience to defoliation and to N
410deprivation, ii) critical N decline during stand growth, iii) self-thinning and iv) trait mediated
411species productivity response to defoliation and N deprivation. Furthermore, simplified
412versions of the model lacking processes controlling plant plasticity and population plasticity
413display a lower net primary productivity as compared to the full plastic model.

414

4154.1. Emergent properties of the model

416 At full complexity, the model presents emergent properties, which account for four well-
417 established empirical laws.

418 First, the GEMINI model re-establishes a functional balance after a disturbance caused by
419 defoliation and after a stress caused by N deprivation. After a defoliation event, a preferential
420 partitioning of substrates first to leaf proteins and then to shoot structures is induced at the
421 expense of roots. This response to defoliation replenishes leaf N content and increases leaf
422 area. Conversely, after N deprivation, preferential partitioning to roots takes place and the
423 activity of root transporters is de-repressed which also contributes to increased N uptake,
424 thereby restoring a functional equilibrium and a coordination of leaf photosynthesis. Hence,
425 through changes in the relative sizes and physiological activities of roots and shoots, plant
426 growth will again be co-limited by multiple resources capture (photosynthetically active
427 radiation, atmospheric CO₂ and inorganic N).

428 Second, the model accounts for the decline in critical N concentration during stand
429 regrowth. Even when there is ample supply of N, plant shoot N concentration declines during
430 growth within dense canopies. This observation led to the development of a law relating
431 critical shoot N concentration (see Methods) and stand dry matter accumulation by a negative
432 power function (Lemaire et al., 2008). For LAI values below ca. 5, this empirical law is well
433 accounted for by the model. This shows that when leaves become gradually shaded, changes
434 in leaf proteins to structure ratio support the hypothesis of leaf photosynthesis coordination
435 (Maire, 2009). Through changes in the *Q* partitioning variable, an increasing fraction of
436 shaded leaves induces the simulated decline in shoot N concentration during canopy growth.
437 In contrast, simulated N content of leaves in full light at the top of the canopy remain constant
438 (data not shown), in agreement with previous measurements (Gastal and Lemaire, 2002). At
439 high LAI values (above 5), the empirical critical N content is slightly above the coordinated

440simulated leaf N content. Overall, it is remarkable that the value and plasticity of C-N
441stoichiometry (see Gruber and Galloway, 2008) during autotrophy is an emergent property of
442coordinated resource acquisition by plants.

443 Third, self-thinning, a well-established empirical law is also predicted. The self-thinning
444rule relates plant mass to plant density in crowded, even-aged stands by a power-law equation
445with a negative exponent which is usually close in absolute value to $3/2$. The rule is widely
446accepted as an empirical generalization and quantitative law that applies across the plant
447kingdom (*e.g.* Sackville-Hamilton et al., 1995; West et al., 1999). It is remarkable that the
448combination in the GEMINI model of detailed ecophysiological and morphogenetic processes at
449the individual plant scale results in a self-thinning rule relating size and density of tillers
450across grass species. Interestingly, both the model and the measurements show a negative
451exponent close to one, and therefore substantially lower than the $3/2$ exponent (but see
452Enquist and Niklas, 2002). This could be caused by the physiological integration among tillers
453within clonal grasses which tends to reduce tiller mortality within crowded stands (De Kroon
454et al., 1992).

455 Finally, another emerging model property concerns its ability to explain some of the
456observed trait mediated species productivity responses to defoliation and N deprivation. The
457correlation between the log-response ratio of *ANPP* to cutting frequency and *SLA* is in good
458agreement with previous observations (Caldwell, 1981; Westoby, 1999) showing that high
459*SLA* favors fast leaf regrowth and hence a tolerance response to defoliation, by increasing the
460rate of leaf recovery (Gross et al., 2007). Similarly, the negative correlation between the log-
461response ratio of *ANPP* to N supply and plant height is consistent with the positive
462relationship which was found between plant height and N conservation with the same grass
463species (Maire et al., 2009).

464

4654.2. Role of plasticity

466The plasticity of traits can be influenced by allometric or physiological constraints and some
467species might be less plastic than others depending on their traits (Givnish, 2002; Enquist and
468Niklas, 2002; Weiner, 2004). However, to date, few studies have investigated relationships
469between trait plasticity and the variations of physiology, morphology and growth across plant
470species (Ackerly and Sultan, 2006).

471 The present modeling study supports the hypothesis that plasticity favors the resilience
472along nutrients and disturbance gradients of plant production and competitive ability (Figures
4736, 7, 8) in agreement with previous reports (*e.g.* Soussana and Lafarge, 1998). With an
474individual centered-model such as GEMINI, suppressing axis demography (RP₁ version) halved
475the overall mean *ANPP* simulated by the model. Plastic adjustments in tiller density have been
476observed in response both to cutting frequency and to nitrogen supply (Lemaire and
477Chapman, 1996). Indeed, the negative exponent between tiller size and density shows that
478these two traits co-vary both within and across grass species. Imposing a constant tiller
479density, leads either to excess C and N substrates (under environmental conditions favorable
480for growth), or to substrate deficiency whenever resources become too limited to support the
481tiller population (data not shown).

482 Although suppressing shoot morphogenesis simulation (RP₂) did not affect significantly
483*ANPP*, suppressing both root morphogenesis and axis demography (RP₃) reduced by a factor
484of four *ANPP* in comparison to the full model. Therefore, root architecture and turnover
485appear to have a major role in an individual-centred model, since they contribute to the
486stability of yield along resource and disturbance gradients. Finally, further suppressing growth
487coordination (RP₅ and RP₆) leads to a mean *ANPP* that is divided by a factor of 1.25 or more
488compared to the full model, which underlines the major role of growth and photosynthesis
489coordination (Fig. 8).

490 These simulations reveal that although simple compartment-based models may be
491 successful at predicting the instantaneous fluxes exchanged between vegetation and the
492 environment, they are not applicable at the individual plant and population scales. Given the
493 large variability in resource levels and in microclimate experienced by individual plants
494 within stands, most assumptions of simple models (*e.g.* constant radiation and nitrogen use
495 efficiencies) do not hold at this scale (Faurie et al., 1996; Gastal and Lemaire, 2002). In
496 contrast, individual centered models show that plasticity in the form and function of
497 individual plants stabilizes productivity, light interception and N uptake, as well as radiation
498 and N use efficiencies (data not shown).

499 When applying the full model to binary mixtures, simulated grass species dominance was
500 consistent with observations of:

501- an increased dominance of grass species which have high plant stature and
502 conservative traits (such as *F. arundinacea*) at low compared to high cutting frequencies,
503 compared both to short and to tall exploitative grasses (*e.g.* *A. odoratum* and *A. elatius*),
504 (Louault et al., 2005; Pontes et al., 2011);

505- an increased dominance of tall vs. short exploitative grass species (*A. elatius*
506 vs. *A. odoratum*) at low compared to high cutting frequencies (Grime, 1979; Pontes et al.,
507 2011).

508 Without an explicit root and shoot morphogenesis, grass species dominance was not altered
509 along a disturbance gradient. Under increased disturbance by cutting, species ability to rapidly
510 emit new leaves is an important trait that favors competitive ability for light capture
511 (Cingolani et al., 2005). Therefore, without explicit shoot morphogenesis, this capacity is lost
512 and changes in dominance with cutting frequency are not simulated adequately anymore.

513

514

5164.3. Model complexity

517 There is a common understanding that the complexity of a particular system is linked to the
518 difficulty in predicting the system properties despite a detailed knowledge of the system
519 elements and their relationships (Weaver, 1948; Heylighen, 2008). Complexity can be seen
520 either as disorganized or as organized. The latter case applies to our study since we consider
521 non-random and correlated interactions between a range of processes at the root, shoot, plant,
522 population, community and ecosystem scales. We have retained the emergence concept since
523 our simulated system shows plasticity properties which are not dictated by the elementary
524 parameters which are used for modeling these processes. To understand such organized
525 complexity with emergent properties computer simulation was necessary (Hill, 1996).

526 In this way, we changed the granularity of different submodels of GEMINI in order to
527 test their pertinence for the plant fitness in a given environment. This has been partially
528 integrated in the software architecture by activating / deactivating some submodels (*e.g.* leaf
529 and root architectures) that are replaced by more simplistic behaviors. However this
530 replacement is not fully automated in GEMINI, and it should be interesting for a mechanistic
531 model like GEMINI to push away the degree of granularity at will. The difficulty of changing
532 model granularity lies in the issue of coupling models. Coupling models requires a framework
533 and a methodology of development (Davis, 2001) accounting for the exchange of data
534 between models which should be considered itself as a model (Winiwarter, 2005) as well as
535 for the ordering of variables during the integration process, because a dependency between
536 variables implies an order of computation. This issue requires being able to analyze the
537 formulas when coupling models to find the dependencies between variables and set up a new
538 ordering in the integration process. As GEMINI is developed in C++ language, one can consider

539designing an EDSL (Embedded Design Specific Language) based on metaprogramming and
540operators overloading (Fowler, 2010).

5415. CONCLUSION

542The GEMINI model provides a consistent trait-based mechanistic framework for modeling the
543role of grass diversity and plasticity on community dynamics and ecosystem functioning. In
544this paper, we have shown from *in-silico* experiments the role of morphological (root and
545shoot morphology) and physiological (leaf N content, leaf photosynthesis) plasticity, as well
546as population (axis density) plasticity, for plant population fitness (*i.e.* net primary
547productivity) across resource, disturbance and competition gradients. Moreover, we have
548shown that model versions for which plasticity has been suppressed are not able to reproduce
549observed changes in net primary productivity across environment and competition gradients.
550Therefore, the details of physiological and morphological mechanisms allowing adaptive
551plasticity in the GEMINI model are both necessary and sufficient (in agreement with the
552parsimony principle) to simulate major trends in perennial grasses productivity and
553dominance. This modeling experiment shows that along environmental and competition
554gradients the plasticity of plant form and function contributes to maintain the coordination of
555multiple resource capture and, hence, to sustain productivity and dominance.

556

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691 **TABLE CAPTIONS**

692 **Table 1.** Parameter calibration of GEMINI for reduced plasticity versions (RP₁₋₆). The
693 parameterization of the full plasticity version (FP) is reported by Soussana et al. (2012). A)
694 Modeling experiment evaluating the role of plant plasticity. The full GEMINI model (FP) was
695 compared with reduced demographic and morphogenetic plasticity (from RP₁ to RP₄) and
696 with reduced coordination of growth (RP₅ and RP₆) versions. D_{sp}, indicates that a dynamic
697 variable is calculated by the model. P_{sp}, indicates that a parameter has been calibrated for each
698 species using pseudo-equilibrium FP output variables for the C- N⁺ experimental treatment
699 (see Methods). B) Species-specific parameter values (P_{sp}) in reduced plasticity versions.
700 Abbreviations: *intcl*, clonal integration; *Tsen₀*, axis lifespan; *q₁* and *q₂*, power coefficients
701 varying the degree of control on partitioning between shoot and root structures and between
702 shoot structures and leaf proteins, respectively; *C_H*, leaf canopy density; *LAR*, leaf area ratio;
703 *theta*, leaf angle; *TShoot_{sen}*, shoot senescence rate; *TRoot_{sen}*, root senescence rate; *lwr*, root
704 area ratio. nd; not determined.

705

706 **Table 2.** ANOVA (General Linear model) for the effects of plant species (*A. odoratum*, *A.*
707 *elatius* and *F. arundinacea*), plant plasticity (FP, RP₁ to RP₆ versions of the model, see
708 Methods), cutting frequency, incident light and nitrogen supply factors on simulated above-
709 ground net primary productivity (*ANPP*), fraction of absorbed photosynthetically active
710 radiation (*FAPAR*) and nitrogen uptake rate (*Su*). A) Monocultures, B) Binary mixtures.
711 Abbreviations: df, degree of freedom; Expl. Var., percentage of variance explained; ns, not
712 significant.

713

714 **FIGURE CAPTIONS**

715

716 **Figure 1.** Conceptual design of a modeling experiment for evaluating the role of plant
717 plasticity. Aboveground net primary productivity (ANPP) is compared between full model
718 (FP), reduced demographic and morphogenetic plasticity model versions (RP₁ to RP₄) and
719 reduced coordination of growth (RP₅ and RP₆) model versions.

720

721 **Figure 2.** Effects of a cut (at 5 cm height on day 0) and of N deprivation (from 0.25 to 0.05
722 gN m⁻² d⁻¹ on day 110) on the *P* and *Q* variables partitioning assimilates between shoot and
723 root structures, and between shoot structures and leaf photosynthetic proteins, respectively.
724 Simulations were run with *D. glomerata* under a constant environment. Note that small
725 oscillations in *P* and *Q* dynamics after disturbance by cutting and N deprivation are caused by
726 changes in leaf and in root numbers (emission and mortality).

727

728 **Figure 3.** Simulated and empirical relationships between shoot N concentration and shoot dry
729 matter during regrowth after a cut (open circles) for the C-N+ treatment. Open circles show
730 simulation results. The solid line shows the empirical law relating critical shoot N
731 concentration (*Y*, %) and shoot dry-matter (*X*, t DM ha⁻¹) as $Y = 4.8 X^{-0.32}$ (Lemaire et al.,
732 2008). The dashed line shows the fit of a power law to simulated results for shoot dry-matter
733 values above 2.5 t DM ha⁻¹.

734

735 **Figure 4.** Relationships between simulated mean tiller mass (*W_G*), simulated shoot mass (*W_S*
736 + *W_P*) and simulated mean tiller density (*A*); and between observed shoot mass and observed
737 mean tiller density (*B*) across 13 grass species. Species abbreviations are: *Alopecurus*
738 *pratensis* (*Ap*), *Anthoxanthum odoratum* (*Ao*), *Arrhenatherum elatius* (*Ae*), *Dactylis*

739 *glomerata* (*Dg*), *Elytrigia repens* (*Er*), *Festuca arundinacea* (*Fa*), *Festuca rubra* (*Fr*), *Holcus*
740 *lanatus* (*Hl*), *Lolium perenne* (*Lp*), *Lolium perenne* cultivar (*Cl*), *Phleum pratense* (*Php*), *Poa*
741 *pratensis* (*Pp*), *Poa trivialis* (*Pt*), *Trisetum flavescens* (*Tf*). In A, simulated relationships for
742 mean tiller mass (W_G) and for shoot mass ($W_s + W_p$) are displayed in capitals and in small
743 letters, respectively. Simulations were run for 10 years in monocultures at 3 cuts per year and
744 for 360 kgN ha⁻¹ yr⁻¹ N fertilizer supply. Slope and intercepts of SMA regressions were
745 calculated according to Warton *et al.* (2006). In B, the observations of tiller density and shoot
746 mass of grass species were measured under equivalent management in the site of Theix and
747 were fully commented in Pontes *et al.* (2007) and in Soussana *et al.* (2012).

748

749 **Figure 5.** Relationships between plant functional traits and above-ground net primary
750 productivity (ANPP) response (log response ratio, LNRR, Suding *et al.* 2003) to management
751 changes of 12 grass species simulated by GEMINI in monoculture. (A) Relationship between
752 specific leaf area (*SLA*) and response to cutting intensity increase (LNRR(cut), from 3 to 6 cut
753 yr⁻¹); (B) Relationship between plant height and response to N fertilization increase
754 (LNRR(N), from 120 to 360 kgN ha⁻¹ yr⁻¹).

755

756 **Figure 6.** Simulated above-ground net primary productivity (ANPP) of three grass
757 monocultures (*A. odoratum*, *A. elatius*, *F. arundinacea*) along disturbance (cutting frequency:
758 1, 3, 6 and 8 cuts yr⁻¹), nitrogen supply (60, 120 and 360 kgN ha⁻¹ yr⁻¹ from substrate and
759 fertilizer) and light (100, 80 and 60% of incident daily *PPFD*) gradients. The full GEMINI
760 model (FP) was compared with versions increasingly (from RP₁ to RP₆) restricting plasticity
761 and coordination of plant form and function (see Methods). RP₁, no axis turnover; RP₂, same
762 as RP₁ but without explicit root morphogenesis; RP₃, same as RP₁ but without explicit shoot
763 morphogenesis; RP₄, same as RP₁ but without explicit root and shoot morphogenesis; RP₅,
764 same as RP₄ with equal distribution of assimilates to leaf structure and leaf proteins; RP₆,

765 same as RP₄ with equal distribution of assimilates to leaf structure and roots. The effects of
766 plasticity level (P), of environmental gradients (C: cutting frequency, N: nitrogen fertilization
767 level, L: light level) and of their interactions were tested by ANOVA (see SI3 for details) and
768 are shown with their corresponding *p*-level.

769

770 **Figure 7.** Simulated above-ground net primary productivity (ANPP) of binary mixtures of *A.*
771 *odoratum*, *A. elatius* and *F. arundinacea* along a cutting frequency (3, 6 and 8 cuts per year)
772 gradient. Figures in the same row compare the two component species within a binary
773 mixture. The full GEMINI model (FP) was compared with versions increasingly (from RP₁ to
774 RP₆) restricting plasticity and coordination of plant form and function. For abbreviations, see
775 Figure 8.

776

777 **Figure 8.** Simulated plasticity levels ratios for mean above-ground net primary productivity
778 (ANPP) of grass species (*A. odoratum*, *A. elatius* and *F. arundinacea*) in monocultures and in
779 binary mixtures across all N fertilization, cutting regime and light gradients. The plasticity
780 level ratio was calculated as the ratio of a given plasticity level (FP, RP₁ to RP₅) to the lowest
781 plasticity level (RP₆).

782 **Table 1.**

A) Parameter of FP model	FP value	RP ₁ value	RP ₂ value	RP ₃ value	RP ₄ value	RP ₅ value	RP ₆ value
<i>intcl</i>	P _{Sp}	0	0	0	0	0	0
<i>T_{sen0}</i>	P _{Sp}	0	0	0	0	0	0
<i>q₁</i>	3	3	3	3	3	3	0
<i>q₂</i>	3	3	3	3	3	0	3
Output of FP model	FP value	RP ₁ value	RP ₂ value	RP ₃ value	RP ₄ value	RP ₅ value	RP ₆ value
<i>C_H = LAI / H</i>	D _{Sp}	D _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}
<i>LAR = LAI / (D · (W_s + W_p))</i>	D _{Sp}	D _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}
<i>theta = $\frac{theta}{i \text{ layers}}$</i>	D _{Sp}	D _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}
<i>TShoot_{sen} = SA_{sen} / SA</i>	D _{Sp}	D _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}
<i>TRoot_{sen} = RA_{sen} / RA</i>	D _{Sp}	D _{Sp}	P _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}
<i>lwr = RA / RM</i>	D _{Sp}	D _{Sp}	P _{Sp}	D _{Sp}	P _{Sp}	P _{Sp}	P _{Sp}

783

B) Species value (P_{Sp})	<i>C_H</i> m ² m ⁻³ leaf	<i>LAR</i> m ² g ⁻¹ leaf	<i>theta</i> °	<i>TShoot_{sen}</i> d ⁻¹	<i>TRoot_{sen}</i> d ⁻¹	<i>lwr</i> m ² g ⁻¹ root
<i>Alopecurus pratensis</i>	14.58	0.0188	66.8	0.0253	0.0021	0.0557
<i>Anthoxanthum odoratum</i>	20.58	0.0208	59.7	0.0178	0.0179	0.1523
<i>Arrhenatherum elatius</i>	17.95	0.0233	65.0	0.0222	0.0107	0.0614
<i>Dactylis glomerata</i>	23.59	0.0185	70.1	0.0245	0.0087	0.0700
<i>Elymus repens</i>	18.20	0.0195	57.8	0.0240	0.0040	0.0616
<i>Festuca arundinacea</i>	22.77	0.0154	65.0	0.0111	0.0090	0.0914
<i>Festuca rubra</i>	28.64	0.0098	50.4	0.0164	0.0073	0.0865
<i>Holcus lanatus</i>	33.11	0.0246	70.1	0.0185	0.0158	0.1152
<i>Lolium perenne</i>	18.21	0.0179	70.5	0.0195	0.0008	0.0722
<i>L. perenne</i> var. Clerpin	18.99	0.0197	66.3	0.0167	0.0107	0.0625
<i>Phleum pratense</i>	26.36	0.0219	59.4	0.0185	0.0166	0.0944
<i>Poa pratensis</i>	32.76	0.0178	58.2	0.0135	0.0106	0.0903
<i>Poa trivialis</i>	nd	nd	nd	nd	nd	nd
<i>Trisetum flavescens</i>	17.54	0.0194	53.3	0.0250	0.0219	0.1257

784

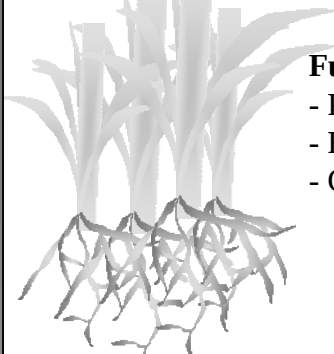
785Table 2

A) Monoculture		<i>DMY</i>		<i>FAPAR</i>		<i>Su</i>	
Factors	df	Expl. Var.	P	Expl. Var.	P	Expl. Var.	P
Species	2	5.25	< 0.001	2.7	< 0.001	24.0	< 0.001
Plasticity	6	24.03	< 0.001	42.2	< 0.001	32.3	< 0.001
C	2	10.03	< 0.01	6.3	< 0.001	0.7	< 0.01
N	2	21.91	< 0.001	11.8	< 0.001	27.8	< 0.001
Light	2	0.47	< 0.01	3.7	< 0.001	3.0	< 0.001
Species*Plasticity	12	14.24	< 0.001	16.6	< 0.001	5.0	< 0.001
Species*C	6	0.74	< 0.01	-	ns	-	ns
Species*N	4	0.59	< 0.01	-	ns	-	ns
Species*Light	4	0.79	< 0.01	2.7	< 0.001	-	ns
Plasticity*C	18	11.48	< 0.001	-	ns	0.6	< 0.01
Plasticity*N	12	6.58	< 0.001	3.3	< 0.001	2.2	< 0.001
Plasticity*Light	12	2.57	< 0.001	7.5	< 0.001	4.3	< 0.001
C*N	6	1.32	< 0.001	1.0	< 0.01	-	ns
C*Light	6	-	ns	-	ns	-	ns
N*Light	4	-	ns	2.1	< 0.001	-	ns
Total	652	$r^2 = 75.0$	< 0.001	$r^2 = 67.2$	< 0.001	$r^2 = 88.1$	< 0.001

B) Mixture		<i>DMY</i>		<i>FAPAR</i>		<i>Su</i>	
Factors	df	Expl. Var.	P	Expl. Var.	P	Expl. Var.	P
Mixture	2	1.7	< 0.001	0.5	< 0.01	1.3	< 0.001
Species	2	0.9	< 0.001	-	ns	30.2	< 0.001
Plasticity	6	28.9	< 0.001	24.4	< 0.001	33.2	< 0.001
C	2	9.3	< 0.001	2.5	< 0.001	1.0	< 0.001
N	2	9.8	< 0.001	2.7	< 0.001	21.3	< 0.001
Light	2	0.9	< 0.001	-	ns	3.0	< 0.001
Mixture*Plasticity	12	3.9	< 0.001	8.6	< 0.001	1.7	< 0.001
Mixture*C	6	0.7	< 0.001	2.5	< 0.001	0.2	< 0.01
Mixture*N	4	0.6	< 0.001	-	ns	0.2	< 0.001
Mixture*Light	4	-	ns	-	ns	-	ns
Species*Plasticity	12	20.6	< 0.001	39.2	< 0.001	2.7	< 0.001
Species*C	6	4.5	< 0.001	12.3	< 0.001	1.0	< 0.001
Species*N	4	1.9	< 0.001	3.3	< 0.001	0.8	< 0.001
Species*Light	4	-	ns	-	ns	0.1	< 0.05
Plasticity*C	18	7.6	< 0.001	1.6	< 0.05	1.8	< 0.001
Plasticity*N	12	4.8	< 0.001	1.7	< 0.001	0.7	< 0.001
Plasticity*Light	12	2.6	< 0.001	-	ns	0.8	< 0.001
C*N	6	1.0	< 0.001	-	ns	0.2	< 0.01
C*Light	6	0.4	< 0.05	-	ns	-	ns
N*Light	4	-	ns	-	ns	-	ns
Total	1139	$r^2 = 67.9$	< 0.001	$r^2 = 54.6$	< 0.001	$r^2 = 89.1$	< 0.001

Decreasing the degree of model complexity and plant plasticity

Full plasticity



Full plasticity integrates:

- Population dynamic
- Root and shoot morphogenesis
- Coordination of growth between:
 - shoot and root structures
 - shoot structures and leaf proteins

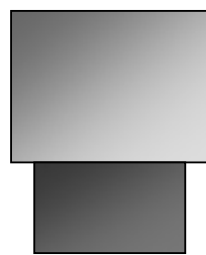
Suppressing axes demography



Level 1 of reduced plasticity (RP₁):

Parameters of clonal integration (*intcl*) and lifespan (T_{sen0}) of an axis set to zero resulting in constant axes density

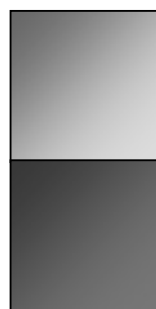
Suppressing shoot and root morphogenesis



Levels 2- 4 of reduced plasticity (RP₂₋₄):

- RP₂: Root morphogenesis is replaced by area-mass root ratio (*lwr*) and root senescence rate ($T_{Root_{sen}}$) parameters
- RP₃: Shoot morphogenesis is replaced by area-mass leaf ratio (*LAR*), shoot senescence rate ($T_{Shoot_{sen}}$), leaf canopy density (C_H) and leaf angle (*theta*) parameters
- $RP_4 = RP_2 + RP_3$

Suppressing coordination of growth

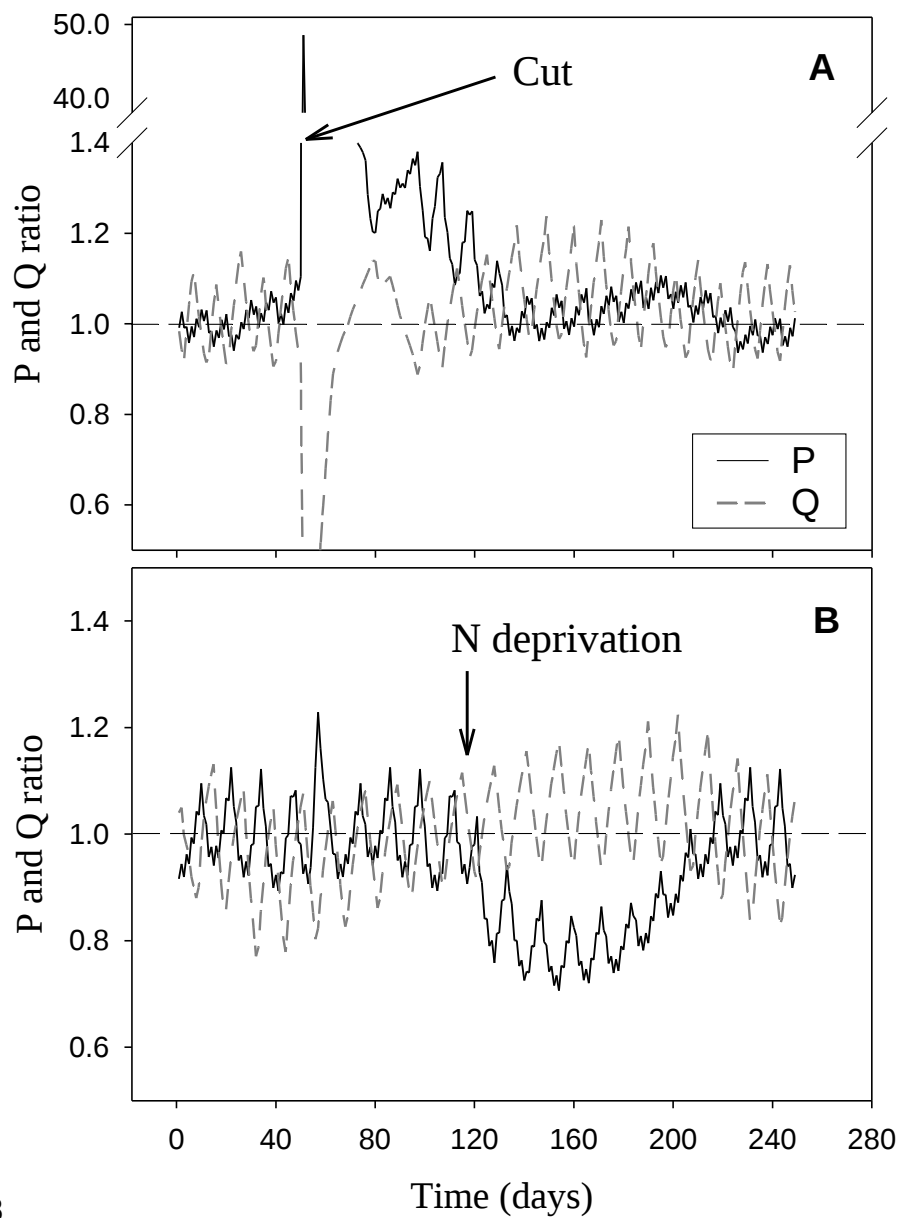


Levels 5-6 of reduced plasticity (RP₅₋₆):

- RP₅: Plastic adjustment of growth between shoot and root structures is suppressed by equally allocating assimilates between compartments (q_2 sets to 0)
- RP₆: Plastic adjustment of growth between shoot structures and leaf proteins is suppressed by equally allocating assimilates between compartments (q_1 sets to 0)

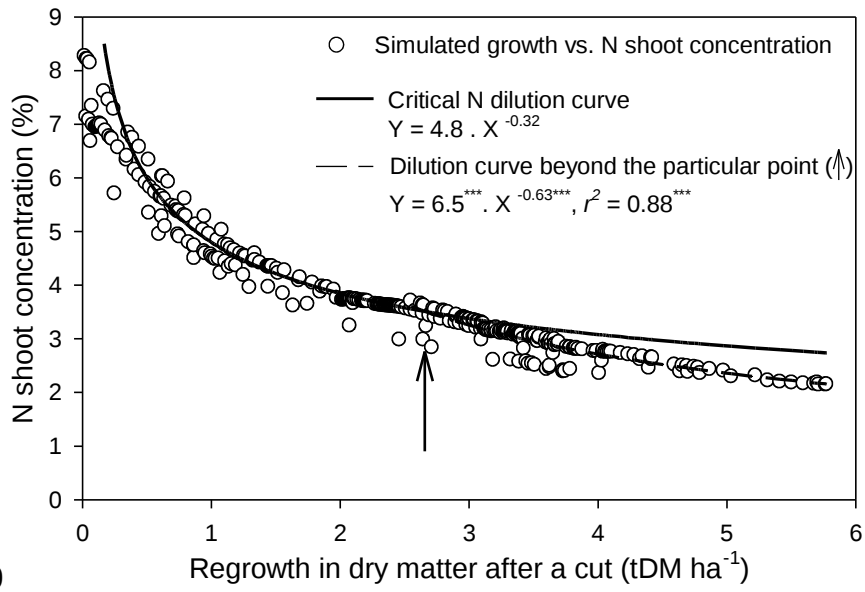
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787Figure 1

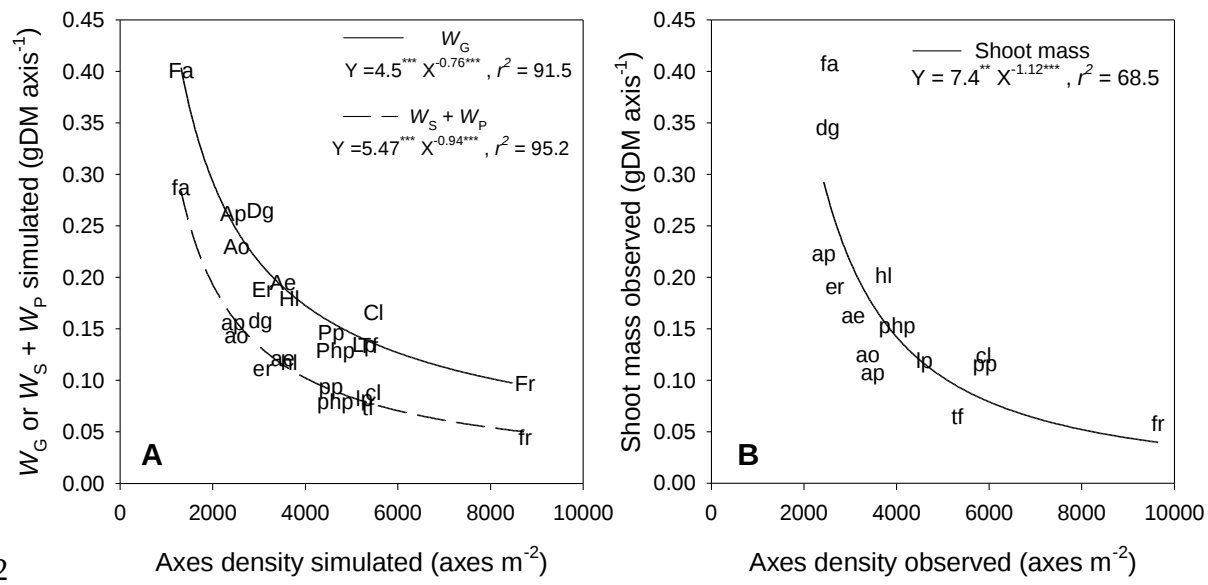


788

789 **Figure 2**

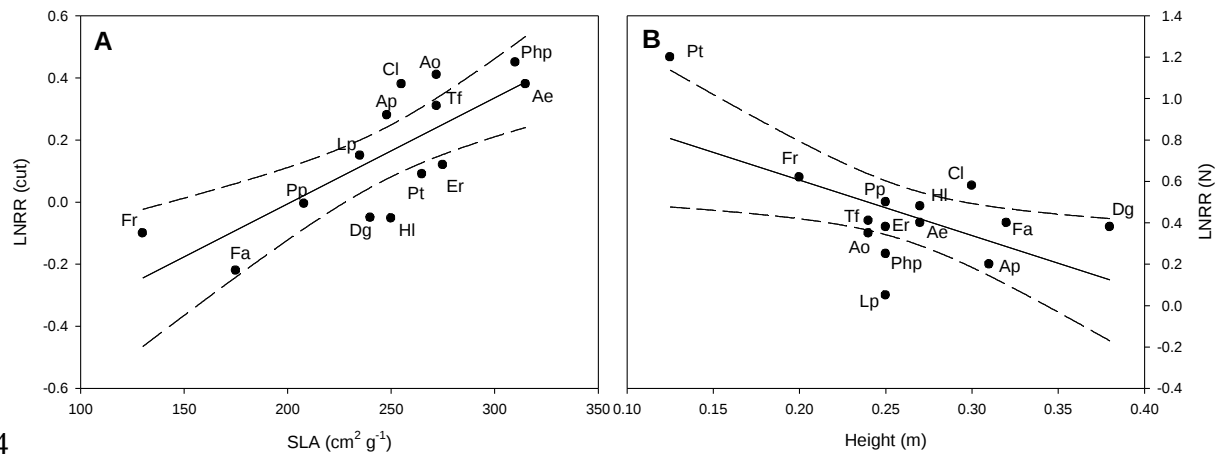


791 **Figure 3**



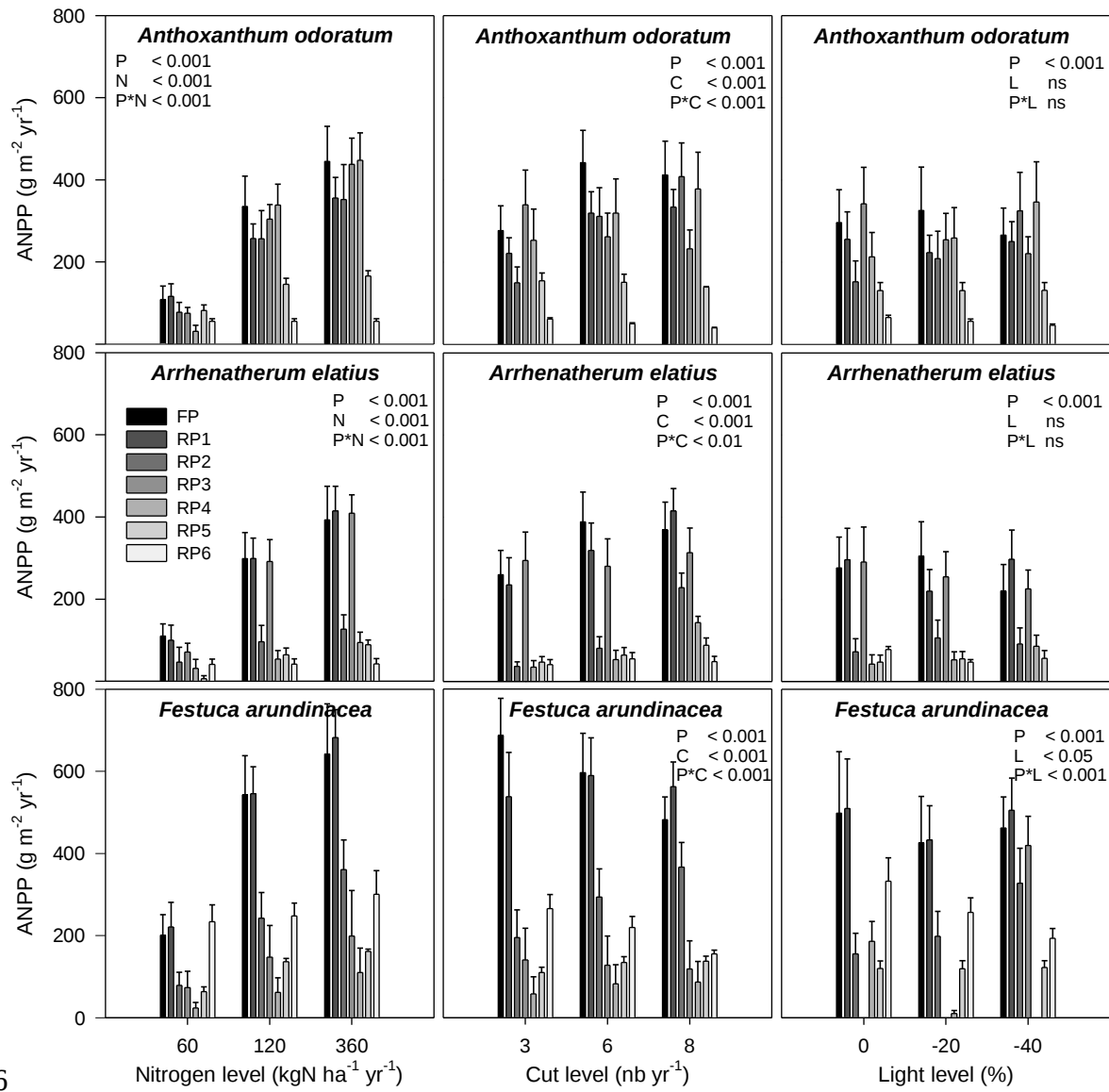
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793 **Figure 4**



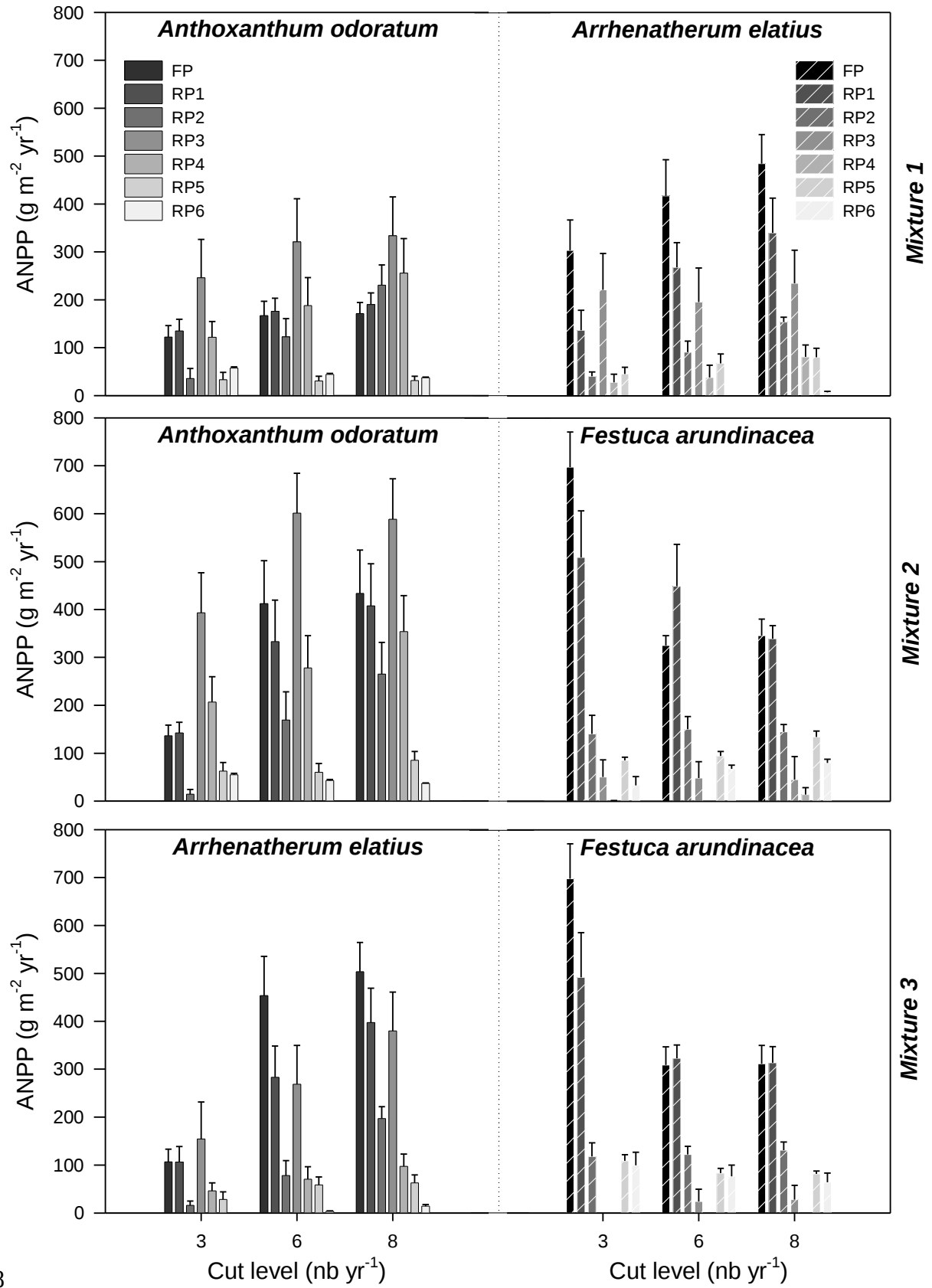
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795 Figure 5



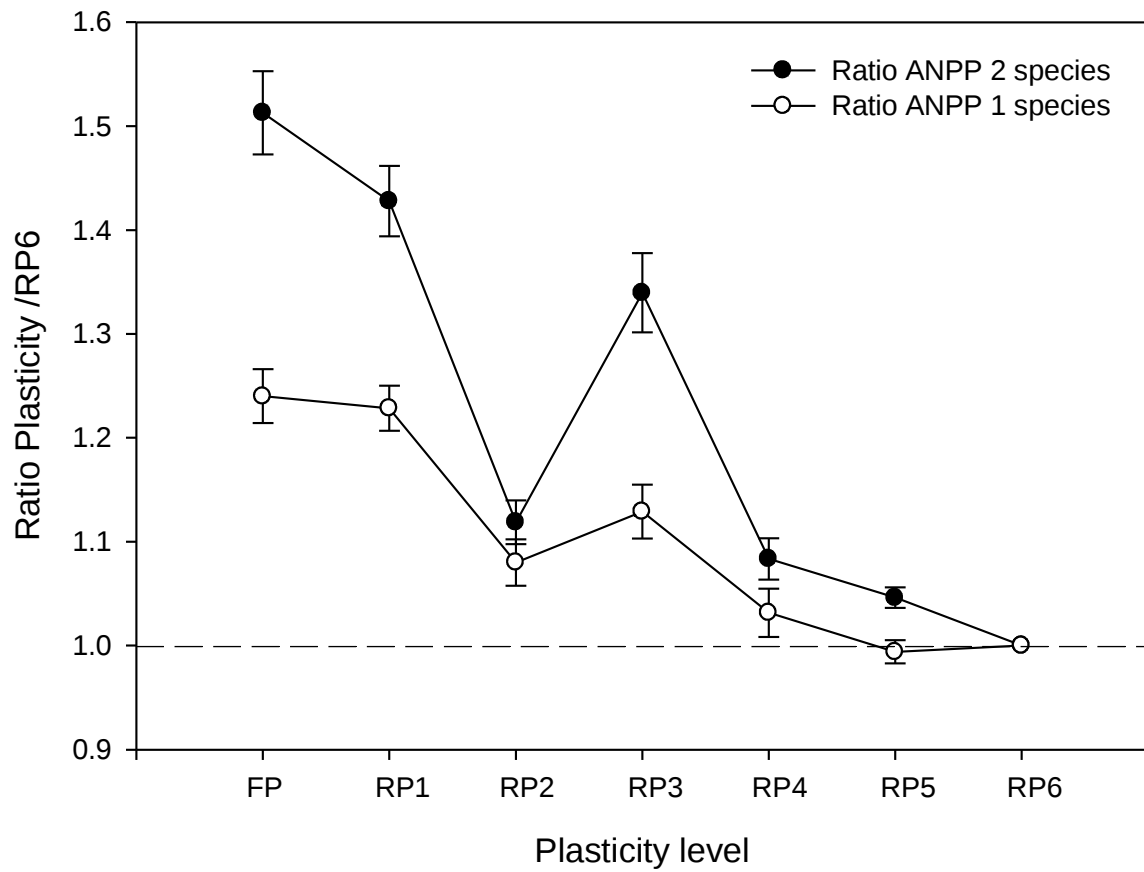
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797 **Figure 6**



798

799 **Figure 7.**



800

801 **Figure 8**