

## Assessing Seed Mixtures for Roadside Revegetation – Richness and Origin as Predictors for Erosion Control

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### ABSTRACT

Roadside revegetation practices have evolved significantly in recent decades, spurred by the need for more reliable and cost-efficient operations and escalating concerns regarding biodiversity integration into large land-planning projects. While the use of rich and locally-sourced seed mixtures for revegetation is being considered with a rising interest to provide ecosystem services and resiliency, their efficacy in meeting practitioners' erosion-control expectations remains underexplored. This study addressed this gap by investigating the erosion-control potential of six seed mixtures, categorized into three compositions with varying levels of richness (standard < competitive < biodiversity) and sourced from local and non-local origins, in a controlled greenhouse environment. For this purpose, the effect of these modalities on vegetation cover, plant density and root biomass production was assessed over a period of 118 days. During the establishment phase, while the effect of the origin on cover was not conclusive, the richer Biodiversity composition achieved faster ground cover, attributed to the presence of large-leaved forbs. The overall density of plants was lower in the richer mix compared to the two others, but significantly higher in its local version. The findings underscored trade-offs between vegetation cover and density, driven by intra- and inter-specific competition processes, particularly related to access to light. Root biomass production was influenced by the origin of the seeds, with local mixes yielding higher biomass, particularly visible in the richer composition. In spite of growing conditions supposed to favor cultivars, wild and locally-sourced seeds showed promising results, advocating their broader adoption in roadside revegetation efforts. These findings provide insights for practitioners to optimize revegetation strategies and enhance roadside ecosystem resilience in the face of changing environmental conditions. In situ field trials should now be carried out to confirm these promising results obtained under controlled conditions for roadside management and ecological restoration.

**Keywords:** seed provenance, species composition, greenhouse experiment, roadside, revegetation, plant cover, erosion control.

### INTRODUCTION

Roadside revegetation practices have undergone a lot of changes in the last decades, partially due to the birth and growth of the “road ecology” research field, as well as increasing concerns regarding the acceptability and integration of biodiversity into the design of large land-planning projects [Forman et al., 2003]. These evolutions are driven by factors that are external to land-planning companies, namely the evolution of environmental laws [Alligand et al., 2018;

MEDDTL, 2012; Morgan, 2012] as well as internal factors like the economic interests for developing innovative techniques and businesses.

A broad range of objectives are associated with revegetation operations, like (1) establishing a plant cover and ensuring that it is maintained over time for geotechnical purposes, (2) maintaining or increasing biodiversity levels by controlling invasive species, establishing ecological connectivity and functionally diverse communities, (3) increasing the public acceptability of projects in regard to landscape integration and

efforts concerning environmental aspects, (4) ensuring user safety by maintaining visibility for the road users notably. From there, practitioners have to choose seed composition and characteristics, mainly on the basis of their availability and cost-effectiveness, as well as their ability to germinate and establish a vegetation cover under certain conditions [Federal Highway Administration, 2007a; Soper, 2019].

In this regard, the use of rich mixtures of native species (i.e. indigenous to a given region) for roadside revegetation practices has developed since the 1970s in the USA and other countries as a means of meeting conservation and ecosystem services provision goals, as well as other technical and economic objectives [Federal Highway Administration, 2007b; Forman et al., 2003; Soper, 2019]. More and more practitioners are now going further by prioritizing the use of locally sourced seeds (i.e. species that are collected in the biogeographical area in which they are reimplanted) for ecological restoration and revegetation operations, following guidelines such as the ones from the Society for Ecological Restoration [Bochet et al., 2010; Henry et al., 2011; Huc et al., 2022; Pedrini and Dixon, 2020; Rogers and Montalvo, 2004]. Many recent studies have explored the potential benefits associated with the use of locally sourced and genetically diverse seeds. Among these benefits, (1) the better local adaptation and establishment of the seeded populations reduces the risks of technical failure [Bucharova et al., 2017; Grossman and Rice, 2012; Krautzer et al., 2011; Vander Mijnsbrugge et al., 2010] and (2) the avoidance of alien invasive species introduction prevents practitioners from potential future added management costs; (3) the better alignment with local commensal or mutualist species in respect of their phenology [Bucharova et al., 2017; Sackville Hamilton, 2001; Vander Mijnsbrugge et al., 2010], and other (4) functional traits [Gadoum et al., 2007; Henry et al., 2011], and (5) local populations genetic diversity [Keller et al., 2000] contribute to the restoration or conservation of local biodiversity, as well as to the adaptation to the effects of climate change.

These new considerations, relating to the environment in and around development areas, the biodiversity and adaptation processes, have not replaced the technical issues that practitioners must address. Rather, they have added to them. On roadsides, for example, it is essential that vegetation quickly contribute to maintaining the soil

on slopes, to avoid jeopardizing the infrastructure and safety of the road. Indeed, slopes of road embankments are prone to diverse forms of wind and water erosion. The water erosion is constituted of several processes including: (i) splash erosion, (ii) sheet and interrill erosion, as well as (iii) rill and gully erosion. Splash erosion is due to the impact of raindrops causing the soil particles to detach, leading to runoffs. Several studies have established a positive relationship, either exponential or linear between vegetation cover and a reduction in splash erosion [Bochet et al., 2002; Flanagan and Nearing, 1995; Knisel, 1980; Morgan et al., 1998; Thornes, 1985; Wischmeier and Smith, 1978]. This is because the presence of a canopy considerably reduces the velocity of raindrops and thus their kinetic energy when hitting the ground, breaking up the droplets, and causing losses of water volume by evaporation. This effect is modulated by the morphological characteristics of a plant (height, leaf surface, orientation and rigidity). Bochet et al. (2002) showed, for example, that stiff and dense tussocks, shrubs, or plants producing large amounts of litter are more effective at mitigating splash erosion than smaller, deciduous species. Some studies tried to establish a minimum plant cover in order to significantly reduce erosion rates, but it seems to greatly vary depending on the edaphic and topographic conditions, ranging from 10% [Abrahams et al., 1988] to 70% [Dinger, 1997]. The cover percentage usually expected by construction companies is around 20% in the first year and 50% in the second (Pierre Grasset, Vinci Autoroute, personal communication).

Sheet and interrill erosion are the transport and loss of fine surface particles by shallow water flow, which can be worsened by mass movements. Rill and gully erosion corresponds to the formation of small to large channels in which water flows rapidly, resulting in losses of soil in the embankment and water quality in the surrounding environment due to increased turbidity and the transport of pollutants [Gyssels et al., 2005; Morgan, 2005]. The presence of vegetation helps mitigating these erosion types by adding some roughness to the ground, reducing the velocity of surface water flows [Engman, 1986; Petryk and Bosmajian III, 1975; Temple, 1982]. This effect is greater as the vegetation is denser and more uniform. Large and isolated individuals like trees or tussocks can sometimes have the negative effect of redirecting the rainfalls on concentrated areas, leading eventually to higher water velocity and

fewer infiltrations into the ground [Armstrong and Mitchell, 1987; De Ploey, 1982].

The erodibility of the soil also depends on its intrinsic properties, such as aggregate stability, infiltration capacity or shear strength [Cruse and Larson, 1977; Gyssels et al., 2005]. These properties are modified by plant root systems. The studies from [Li et al., 1992a, 1992b] show that plant roots reduce soil erodibility and increase infiltration capacity, leading to less surface water flow and ultimately a reduction in the risk associated with runoff. The natural resistance of the soil to compression combined with the root system resistance to tension ultimately increases its shear strength [Simon and Collison, 2001]. A study by [Tengbeh, 1993] on *Lolium perenne* has established a positive relationship between root density ( $\text{kg}\cdot\text{m}^{-3}$ ) and the soil shear strength. An increased shear strength of the soil reduces its vulnerability to erosion by acting on a number of parameters linked to particles detachment process.

Adding biodiversity considerations to the technical constraints of revegetating embankments is not trivial. Some studies have shown a negative relationship between cover and species richness [Fayiah et al., 2019; Iturrate-Garcia et al., 2016]. By association, these results suggest that revegetation which favors plant biodiversity could increase erosion and adversely affect slope stability. However, other studies suggest that diversified implanted plant communities on road verges could increase establishment and productivity [Lepê et al., 2007], and reduce erosion by diversifying root systems architectures [Fattet et al., 2011; Reubens et al., 2007].

Studies conducted by researchers and feedbacks from practitioners on the use of native species for revegetation include both ecological and bioengineering purposes [Bochet et al., 2010; Federal Highway Administration, 2007a]. Studies specifically oriented towards the use of wild and locally-sourced seed mixtures are mostly focused on conservation and restoration outcomes. To the best of authors' knowledge, no study has examined the consequences of using locally-sourced seed mixtures on practitioners' expectations for limiting erosion. Yet, local adaptations of functional traits within species are likely to favor the germination or growth of individuals [Gya et al., 2023; Leimu and Fischer, 2008]. This study tried to bridge this gap by comparing mixtures of varying specific compositions and origins in their ability to answer the expectations of practitioners

regarding erosion-control and interspecific competitiveness potential. The main question the authors sought to answer is how do the species composition and origin influence the expression of revegetation seed mixtures regarding cover, density, and root biomass. To guide the conducted research, the following hypotheses were tested: (1) in a controlled and favorable environment, grass-rich and non-local mixtures yield higher cover and density during vegetation establishment; (2) locally-sourced seeds provide greater resistance to harsher environmental constraints and interspecific competition; (3) locally-sourced and richer mixtures produce more root biomass, as cultivars of landscape species are often selected with priority given to their above-ground traits.

## METHODS

### Seed mixtures

Six seed mixtures were tested, comprised of three species compositions and, for each, two geographical origins. The species compositions (detailed in Table 1) were:

- standard (S) – a common composition used to vegetate roadside verges in temperate climates, composed of 7 species in 3 families (Poaceae, Fabaceae, Rosaceae),
- competitive (C) – a composition designed to cover the soils quickly and compete effectively with invasive species by depriving them of resources, composed of 12 species in 4 families. The proportion in weight of legumes was higher than in the other mixtures.
- biodiversity (B) – a composition designed to maximize species diversity, aerial and root morphologies, life cycles and flowering periods. This composition was composed of 28 species in 11 families. The proportion of grasses and legumes was lowered to allow better growth of other forbs.

The two geographical origins were local (L) and non-local (NL). The non-local seeds came from the industrial seed production sector and were selected based on their availability with no regard to their geographical origin or whether they were cultivars or not (see Figure 1 for origins by taxon). The local versions of the seed mixtures were produced by the Nungesser Semences company (Erstein, Bas-Rhin, France) from wild seeds harvested in the “north-east zone” as one of the

Type	Species	Variety	Type	Origin
<b>Grasses</b>	<i>Anthoxantum odoratum</i>		Wild	Germany
	<i>Bromus erectus</i>		Cultivar	Canada
	<i>Festuca rubra ssp rubra</i>	Mellori	Cultivar	Germany
	<i>Festuca ovina</i>	Bornito	Cultivar	Germany
	<i>Koeleria macrantha</i>		Cultivar	France
<b>Legumes</b>	<i>Anthyllis vulneraria</i>	Palmir	Cultivar	Czech Republic
	<i>Lotus corniculatus</i>	Baco	Cultivar	Argentina
	<i>Medicago sativa ssp lupulina</i>	Virgo	Cultivar	Denmark
	<i>Onobrychis viciifolia</i>		Cultivar	Russia
<b>Other forbs</b>	<i>Achillea millefolium</i>		Cultivar	New-Zeland
	<i>Anthemis tinctoria</i>	Kelwayi	Cultivar	China
	<i>Centaurea jacea</i>		Cultivar	Hungary
	<i>Centaurea scabiosa</i>		Cultivar	Germany
	<i>Cyanus segetum</i>		Cultivar	Hungary
	<i>Crepis rubra</i>	Rose-Pink	Cultivar	Poland
	<i>Daucus carotta</i>	Purple Kisses	Cultivar	China
	<i>Dianthus barbatus</i>	Tall Single Standard	Cultivar	The Netherlands
	<i>Echium vulgare</i>		Cultivar	Germany
	<i>Knautia arvensis</i>		Cultivar	Germany
	<i>Leucantherum vulgare</i>		Cultivar	The Netherlands
	<i>Malva moschata</i>	Rosea	Cultivar	China
	<i>Papaver rhoeas</i>	Shirley Flowered	Single Cultivar	The Netherlands
	<i>Poterium sanguisorba</i>		Cultivar	France
	<i>Reseda alba</i>	White	Cultivar	China
	<i>Salvia pratensis</i>	Blue	Cultivar	China
	<i>Scabiosa atropurpurea</i>		Cultivar	China or The Netherlands
	<i>Silene vulgaris</i>		Cultivar	Germany
	<i>Stachys byzantina</i>	Pink Woolly Leaves	Cultivar	China
	<i>Thymus pulegioides</i>		Cultivar	The Netherlands

**Figure 1.** Table of origins and varieties of non-local seeds

11 French metropolitan biogeographical regions defined as part of the Végétal<sup>®</sup> brand, a national traceability tool for commercialized wild plants. The brand imposes clear criteria regarding harvesting and production methods [Végétal local, 2023], conservation of genetic diversity, and delineates regions of origin by their ecological, pedological, geological and climatic characteristics, as well as other economic considerations.

The seed mixtures were designed with the help of the Nungesser Semences company to be able to grow in the specifically harsh conditions of road embankments. For some taxa, when the exact equivalent was not available for both origins, the closest equivalent was determined and picked following the order of priority: cultivar > subspecies > species (Table 1). It was considered that these

few differences were not such as to bias the comparison between local and non-local mixtures. All the mixtures were cut to 50% by weight with wheat bran to facilitate the sowing process by hand.

### Experimental design

The experiment was conducted at the University Paris-Saclay greenhouses in Orsay, France, from February to August 2022. The seed mixtures were kept in a cold storage room during three months before sowing to allow vernalization.

Ten pots per mixture were sown by hand at a rate of 10 grams of seeds per square-meter (see Figure 2 for weight/seed number equivalents) for a total of 60 pots, constituting an experiment with 6 modalities repeated 10 times: S-L, S-NL, C-L,



**Table 1.** Composition of the six revegetation mixtures: taxa variations and percentages of seed content. S, C, and B are for standard, competitive, and biodiversity seed composition, respectively

Taxa		Families	Seed content (% of total seed weight)		
Non-local	Local		S	C	B
<b>Grasses</b>					
Overall percentage			88	88	60
Overall richness			3	5	5
<i>Anthoxantum odoratum</i> <sup>d</sup>	<i>Anthoxantum odoratum</i> <sup>b</sup>	Poaceae	-	7	6
<i>Bromus erectus</i> <sup>a</sup>	<i>Bromus erectus</i> <sup>b</sup>	Poaceae	15	15	15
<i>Festuca rubra ssp rubra</i> <sup>a</sup>	<i>Festuca rubra ssp rubra</i> <sup>b</sup>	Poaceae	48	38	20
<i>Festuca ovina</i> <sup>a</sup>	<i>Festuca guestfalica</i> <sup>b</sup>	Poaceae	25	20	12
<i>Koeleria macrantha</i>	<i>Koeleria macrantha</i> <sup>b</sup>	Poaceae	-	8	7
<b>Legumes</b>					
Overall percentage			8	9	6.6
Overall richness			3	3	3
<i>Anthyllis vulneraria</i> <sup>a</sup>	<i>Anthyllis vulneraria</i> <sup>b</sup>	Fabaceae	-	3	1.8
<i>Lotus corniculatus</i> <sup>a</sup>	<i>Lotus corniculatus</i> <sup>b</sup>	Fabaceae	2	-	-
<i>Medicago sativa ssp lupulina</i> <sup>a</sup>	<i>Medicago sativa ssp falcata</i> <sup>b</sup>	Fabaceae	2	1	1.8
<i>Onobrychis viciifolia</i> <sup>a</sup>	<i>Onobrychis viciifolia</i> <sup>c</sup>	Fabaceae	4	5	3
<b>Other forbs</b>					
Overall percentage			4	3	33.4
Overall richness			1	4	20
<i>Achillea millefolium</i> <sup>a</sup>	<i>Achillea millefolium</i> <sup>b</sup>	Asteraceae	-	0.5	0.8
<i>Anthemis tinctoria</i> <sup>a</sup>	<i>Anthemis tinctoria</i> <sup>c</sup>	Asteraceae	-	-	0.5
<i>Centaurea jacea</i> <sup>a</sup>	<i>Centaurea jacea</i> <sup>b</sup>	Asteraceae	-	1.5	2
<i>Centaurea scabiosa</i> <sup>a</sup>	<i>Centaurea scabiosa</i> <sup>b</sup>	Asteraceae	-	-	2
<i>Cyanus segetum</i> <sup>a</sup>	<i>Cyanus segetum</i> <sup>b</sup>	Asteraceae	-	-	4.5
<i>Crepis rubra</i> <sup>a</sup>	<i>Crepis biennis</i> <sup>b</sup>	Asteraceae	-	-	1
<i>Daucus carotta</i> <sup>a</sup>	<i>Daucus carotta</i> <sup>b</sup>	Apiaceae	-	-	1.5
<i>Dianthus barbatus</i> <sup>a</sup>	<i>Dianthus carthusianorum</i> <sup>b</sup>	Caryophyllaceae	-	-	1
<i>Echium vulgare</i> <sup>a</sup>	<i>Echium vulgare</i> <sup>b</sup>	Boraginaceae	-	-	2.5
<i>Knautia arvensis</i> <sup>a</sup>	<i>Knautia arvensis</i> <sup>b</sup>	Caprifoliaceae	-	-	3.5
<i>Leucanthemum vulgare</i> <sup>a</sup>	<i>Leucanthemum ircutianum</i> <sup>b</sup>	Asteraceae	-	0.5	1
<i>Malva moschata</i> <sup>a</sup>	<i>Malva moschata</i> <sup>b</sup>	Malvaceae	-	-	2
<i>Papaver rhoeas</i> <sup>a</sup>	<i>Papaver rhoeas</i> <sup>b</sup>	Papaveraceae	-	-	1
<i>Poterium sanguisorba</i> <sup>a</sup>	<i>Poterium Sanguisorba</i> <sup>b</sup>	Rosaceae	4	-	3
<i>Reseda alba</i> <sup>a</sup>	<i>Reseda lutea</i> <sup>b</sup>	Resedaceae	-	-	1
<i>Salvia pratensis</i> <sup>a</sup>	<i>Salvia pratensis</i> <sup>b</sup>	Lamiaceae	-	-	1.6
<i>Scabiosa atropurpurea</i> <sup>a</sup>	<i>Scabiosa columbaria</i> <sup>b</sup>	Caprifoliaceae	-	-	1.5
<i>Silene vulgaris</i> <sup>a</sup>	<i>Silene vulgaris</i> <sup>b</sup>	Caryophyllaceae	-	0.5	1
<i>Stachys byzantina</i> <sup>a</sup>	<i>Stachys recta</i> <sup>b</sup>	Lamiaceae	-	-	1.5
<i>Thymus pulegioides</i> <sup>a</sup>	<i>Thymus pulegioides</i> <sup>b</sup>	Lamiaceae	-	-	0.5

**Note:** a – cultivars; b – vegetal local branded seeds; c – wild and locally sourced in Rhine basin but non-branded seeds; d – wild but non-local.

C-NL, B-L and B-NL. The pots were round, 60 cm in diameter and 25 cm of potting compost ( $\approx$  70 liters) was placed in it. Two culture compartments were used: (1) an enclosed and glazed growing

compartment (GC) with exposure and temperature control, where watering was done manually; (2) a glazed greenhouse (GH) with ventilation and an automatic watering system. Each culture

Number of seeds		$\Delta$
S - C		-11%
S - B		-13%
C - B		5%

$\Delta$ number of seeds	
<b>Grasses</b>	
S - C	-9%
S - B	33%
C - B	41%
<b>Legumes</b>	
S - C	44%
S - B	52%
C - B	9%
<b>Other Forbs</b>	
S - C	-160%
S - B	-194%
C - B	-149%

Number of seeds			
Grasses	NL	L	$\Delta$
S	2700	2700	<b>0,00%</b>
C	2940	2940	<b>0,00%</b>
B	1931	1931	<b>0,00%</b>
<b>Legumes</b>			
S	80	78	<b>3,22%</b>
C	51	50	<b>2,53%</b>
B	47	45	<b>4,95%</b>
<b>Non-legume forbs</b>			
S	16	16	<b>0,00%</b>
C	145	145	<b>0,00%</b>
B	996	1009	<b>-1,33%</b>

Mean WTS (g)		
Grasses	NL	L
S	1,66	1,66
C	1,60	1,60
B	1,94	1,94
<b>Legumes</b>		
S	10,80	10,85
C	12,27	12,29
B	10,40	10,45
<b>Non-legume forbs</b>		
S	7,00	7,00
C	1,27	1,27
B	2,99	2,82

**Figure 2.** Detail of the differences in seed number per growing pot (a) regardless of the species group among compositions, (b) per species group among compositions and (c) per species group between origins; (d) weight of thousand seeds (WTS) in grams per species group between origins

compartment contained 30 pots, with 5 replicates for each modality. In each compartment, the arrangement of pots was randomized with the constraint that two pots of the same modality could not stand side by side.

## Measurements

Vegetation cover (%) was assessed visually by standing vertically above the pots on days 8, 11, 18, 28, 40, 49, 56, 77, 91, 98, 118. Densities were calculated from the estimation of the abundance of individuals for each species group. Abundance was estimated by counting the individuals present in two  $8.5 \times 8.5$  cm quadrats placed randomly in each pot (i.e. approximately 5.1% of the total surface area). Once the vegetation was too developed for quadrats to be placed, the individuals were counted in a linear strip 5

cm wide from one edge of the pot to the other, passing through the center, in a random direction using strings (i.e. approximately 10.6% of the total surface). Grass species were easy to identify and were counted on days 11, 18, 44, 68, 91, 105. Forbs were counted on days 11, 18, 34, 40, 69, 98, 118, among which legumes were identifiable and counted separately on days 34, 40, 69, 98, 118.

To estimate root biomass, soil samples were collected with a 2 cm wide gouge throughout the depth of the soil, i.e.  $78.54 \text{ cm}^3$  of soil sample per pot. The extracted cores were divided into two parts of equal length: the top half and the bottom half (12.5 cm each). Using tweezers, the fresh roots were then separated from the substrate of each half-core for 15 minutes and then placed in a sealed and identified aluminum foil. The fresh root samples were then soaked for 2 minutes in clear water and removed from any remaining soil,

then weighed using an electronic weighting scale (precision of 0.001 g). The roots were then left to dry for 24 hours at 60 °C and weighed again using the same material.

## Data analysis

Different response variables (cover, densities and root biomass) in various models with a constant set of factors were considered: origin (two-levels factor, fixed effect) mix (three-levels factor, fixed effect), day (fixed effect) and their interactions, and block (two-level factor). The random effect of individual pots was added to address the repetition of measurements. All analyses were conducted in R (v2023.12.0 + 369) using the “stats”, “brms” (v2.20.4), “lme4” (v1.1 - 34) packages. Differences among days, origins and compositions were assessed by Tukey posthoc test using the “emmeans” package (v1.8.8).

The cover variable represents proportional data with values between 0 and 1. The evolution of the cover metric exhibits an initial phase of increase, which is referred to as the growth phase, followed by variations around a plateau, denominated the competition phase. To account for the specific characteristics of each phase, the statistical analysis on cover were performed separately for each phase. In the growth phase, the evolution of cover was modeled using a two-parameter Weibull growth model:  $(1 - \exp(-\exp(lrc) \times t^{pwr}))$  (Eq. 1) with  $x$ , the day. The log rate of change ( $lrc$ ) and the power ( $pwr$ ) parameters act as scale and shape parameters, respectively [Mode, 1985]. The fixed effects modulated both the  $lrc$  and  $pwr$  parameters, while the random pot effect was applied solely to the  $lrc$  parameter. The estimation of this non-linear mixed model was performed in a Bayesian framework using the brms package (v2.20.4). The posterior parameters distribution was used to compute the estimations of times to reach target cover thresholds and compare them. The 20%, 50%, 80% thresholds were selected based on the expectations of land-planners in the context of a road slopes revegetation setting. For phase 2, a binomial generalized mixed model (glmm) was performed to explain the cover by the effect of the factors day, origin and composition and all their tri-wise and pairwise interactions, the bloc effect, and the individuals as a random effect  $(\text{day} + \text{origin} + \text{composition})^3 + \text{bloc} + (1|\text{Indiv})$ .

A linear mixed model was performed using the same factors as previously described for the

cover of phase 2:  $\sim (\text{day} + \text{composition} + \text{origin})^3 + \text{bloc} + (1|\text{Indiv})$  on the density of grasses, legumes and non-legume forbs separately. At day 68–69, the total density of individuals was assessed and a linear model was performed:  $\sim (\text{composition} + \text{origin})^2 + \text{bloc}$ . All density data were log-transformed to achieve more normal distributed errors with constant variance.

The conducted study of the root biomass production was based on the dry mass per volume of soil to eliminate the variation caused by moisture heterogeneity amongst pots at the time of sample collection. The dry mass was analyzed considering the effect of the mix and origin and their interaction, and the effect of bloc biomass data were log-transformed to achieve more normal distributed errors with constant variance.

## RESULTS

### Cover

During the growth phase, the Biodiversity mixes reached all three target cover thresholds (20%, 50%, 80%) faster, followed by the competitive (C) and lastly the standard (S) mixes (Figure 3). The differences among the compositions were significant for the three thresholds (Figure 4). Mixes of non-local origin (NL) reached the three cover thresholds more quickly in B and S, but more slowly in the case of C. However, these differences were only significant for B. Weibull growth model during the establishment phase. S, C, and B are for standard, competitive, and biodiversity seed composition, respectively. NL and L are of non-local and local origins. After day 56 (i.e. the beginning of the competition phase), when plant cover was at its peak for all 6 mixtures, ranging from 98.2% to 99.3% on average per composition, we observed a general trend towards cover loss until day 91, followed by a stabilization from day 91 to 98 and a slight regain at day 118. Overall, the mean cover of all 6 mixtures remained high ( $\geq 90\%$ ) with few differences among them (Figure 5). Comparison between the origin of the mixes revealed a slightly higher overall cover in B-L compared with B-NL, only significant at day 77 ( $p < 0.0001$ ). The cover of C-NL was slightly higher than C-L from day 91 to 118, as was S-NL compared with S-L (only significant at day 118) (Figure 6).

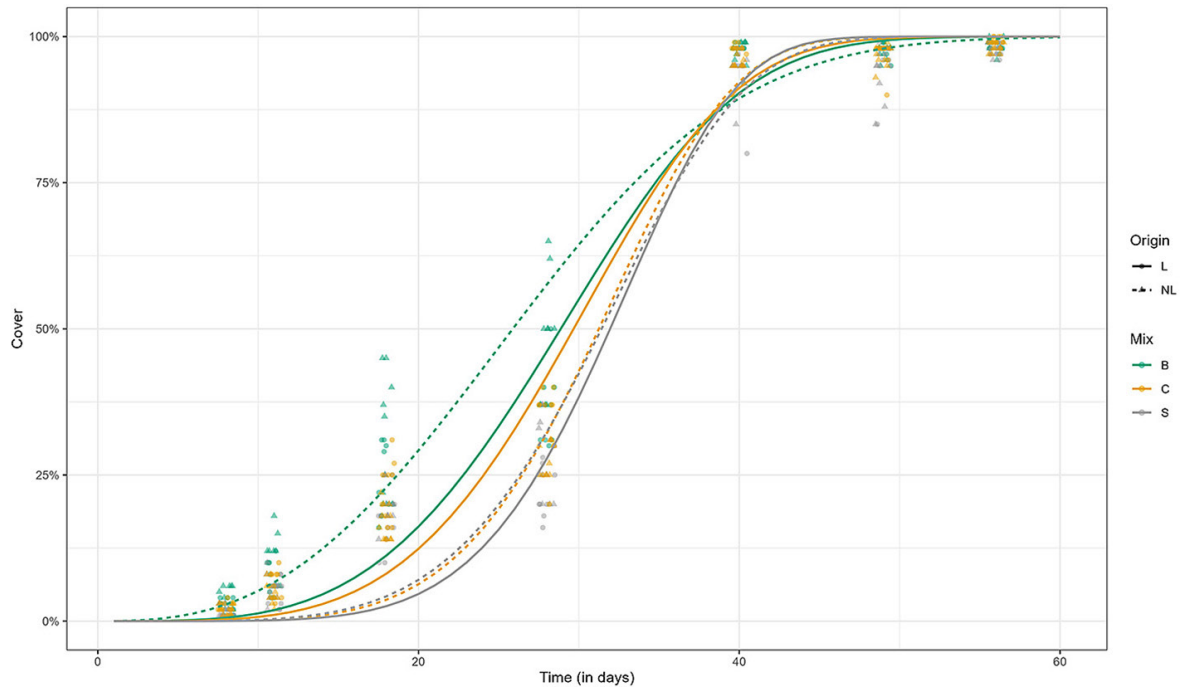


Figure 3. Evolution of the estimated cover (%) in time for all six mixtures following a two parameters

a)

Target cover threshold	Mix1	Mix2	qinf	qsup
20%	C	S	-0.8520585	-0.05136114
	B	S	-1.8316469	-1.04074766
	B	C	-1.3858415	-0.56368586
50%	C	S	-2.6467355	-0.15954227
	B	S	-5.6896150	-3.23285751
	B	C	-4.3048169	-1.75096822
80%	C	S	-6.1455295	-0.37044567
	B	S	-13.2108768	-7.50646269
	B	C	-9.9954753	-4.06562230

b)

Target cover threshold	Mix	Contrast (origins)	qinf	qsup
20%	S	L - NL	-0.2077519	0.32277196
	C	L - NL	-0.5209248	0.02580751
	B	L - NL	0.2001462	0.79375578
50%	S	L - NL	-0.6453365	1.00262130
	C	L - NL	-1.6181402	0.08016544
	B	L - NL	0.6217109	2.46563067
80%	S	L - NL	-1.4984249	2.32801456
	C	L - NL	-3.7572052	0.18613839
	B	L - NL	1.4435681	5.72501713

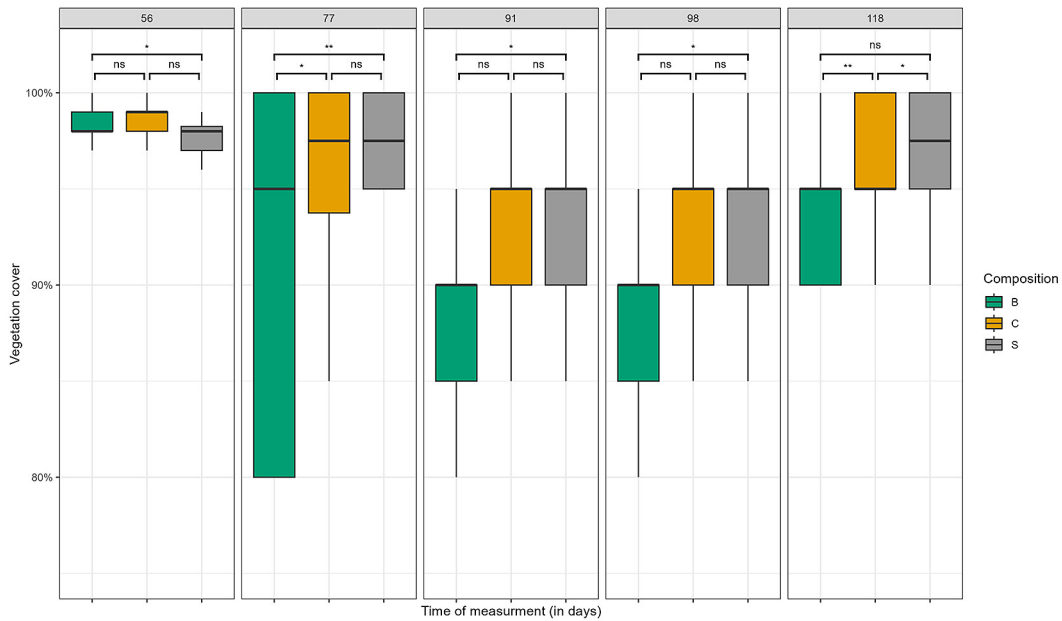
Figure 4. Results of the comparisons among compositions and origins for the estimations of times to reach target cover thresholds (20%, 50% and 80%). The test is significant when 0 is not included in the [qinf : qsup] interval

### Density

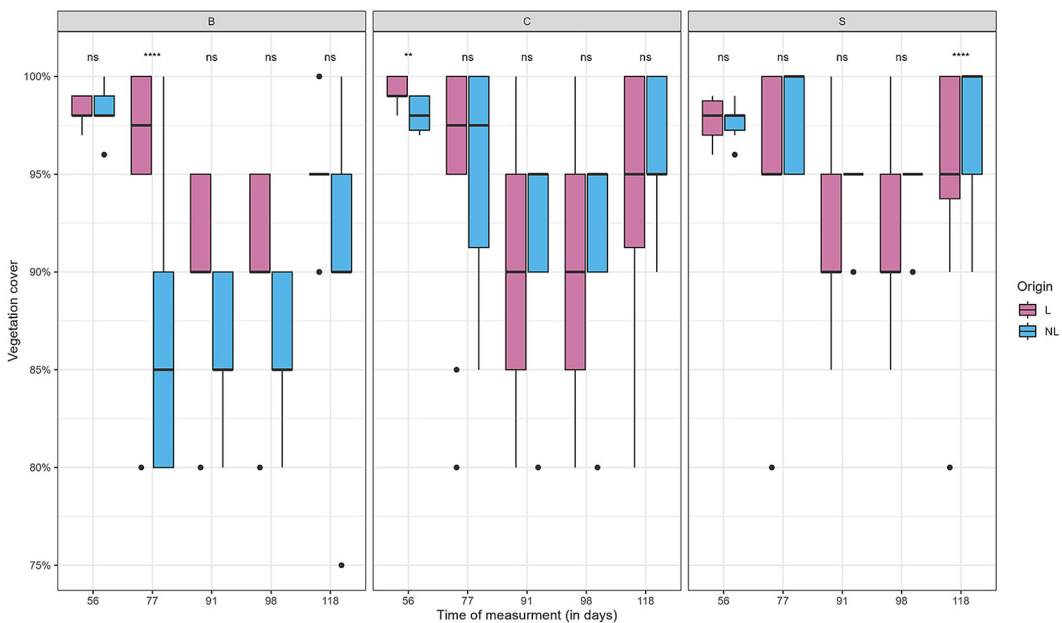
The day × origin, day × composition interactions were present for the density of grasses, legumes and non-legume forbs, with day × composition × origin for the latter. A composition × origin interaction was detected for the total density. At day 68–69, the total

density of plant individuals was significantly lower in B than in C and S. No difference was found between origins for C and S, but the total density was higher in B-L than in B-NL. Across all compositions, the density of grasses followed an overall downtrend throughout the length of the experiment (Figure 8a). As a logical consequence of the differences of





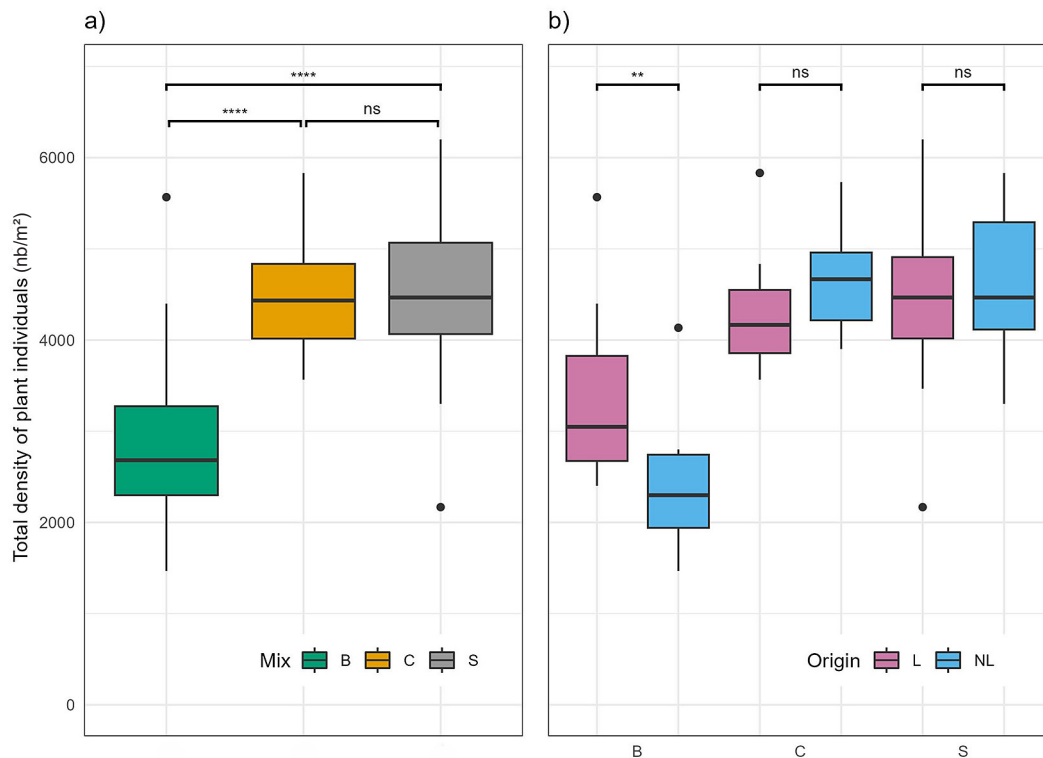
**Figure 5.** Vegetation cover of the three compositions at the times of measurement. Symbols above indicate the level of significance for Tuckey comparisons between among compositions: ns (non-significant), \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ )



**Figure 6.** Vegetation cover of local and non-local versions of all three compositions at the times of measurement. S, C, and B are for standard, competitive, and biodiversity seed composition, respectively. NL and L are of non-local and local origins. Symbols indicate the level of significance for Tukey comparisons between origins: ns (non-significant), \*\* ( $p \leq 0.01$ ), \*\*\*\* ( $p \leq 0.0001$ )

grass seed content among compositions (see Table 1 and Figure 2), the mean density of grasses in B was always significantly lower than in S and C ( $p \leq 0.001$ ). S and C did not show significant differences except at day 91 ( $p = 0.0018$ ) in favor of S (Figure 8a). Throughout the period, except for day 91, B-L

had a slightly higher density of grasses, significant on days 18 ( $p = 0.0062$ ) and 68 ( $p = 0.0029$ ). From day 11 to 44, the L origin also provided a slight edge to S, significant on days 11 ( $p = 0.028$ ) and 44 ( $p = 0.002$ ). The effect of origin was unclear for the C mixes (Figure 5a). Overall, the density of legumes



**Figure 7.** Total density of plant individuals per square meter. S, C, and B are for standard, competitive, and biodiversity seed composition, respectively. NL and L are of non-local and local origins. Symbols indicate the level of significance for Tukey comparisons between compositions and origins: ns (non-significant), \*\* ( $p \leq 0.01$ ), \*\*\*\* ( $p \leq 0.0001$ )

was the highest in S, followed by C and lastly B, with differences decreasing in significance over time (Figure 8b), which is concordant to the number of seeds in each mix (Figure 2). The NL origin favorably impacted the density of legumes across all three compositions with varying degrees of significance from day 34 to 118 (Figure 9b). With high significance from day 34 to 118 ( $p < 0.0001$ ), the density of non-legume forbs was higher in B, followed by C and S. The local origin gave a significantly higher density of non-legume forbs in C on days 34, 40, 98 and 118. For the other species compositions, the effect of origin was unclear (Figure 9c).

### Root biomass

No significant difference was found among modalities regarding dry root biomass production in the bottom-half core samples. In the top-half soil, although not significantly, the root biomass of B and C was 40% and 49 % higher, respectively, than the one in S. The local origin had an overall positive effect on the dry root biomass production ( $p = 0.0035$ ). Considering the 3 species compositions separately, the trend was the

same, significant for B ( $p = 0.006$ ), marginally significant for S ( $p = 0.089$ ), and not significant for C ( $p = 0.4942$ ) (Figure 10).

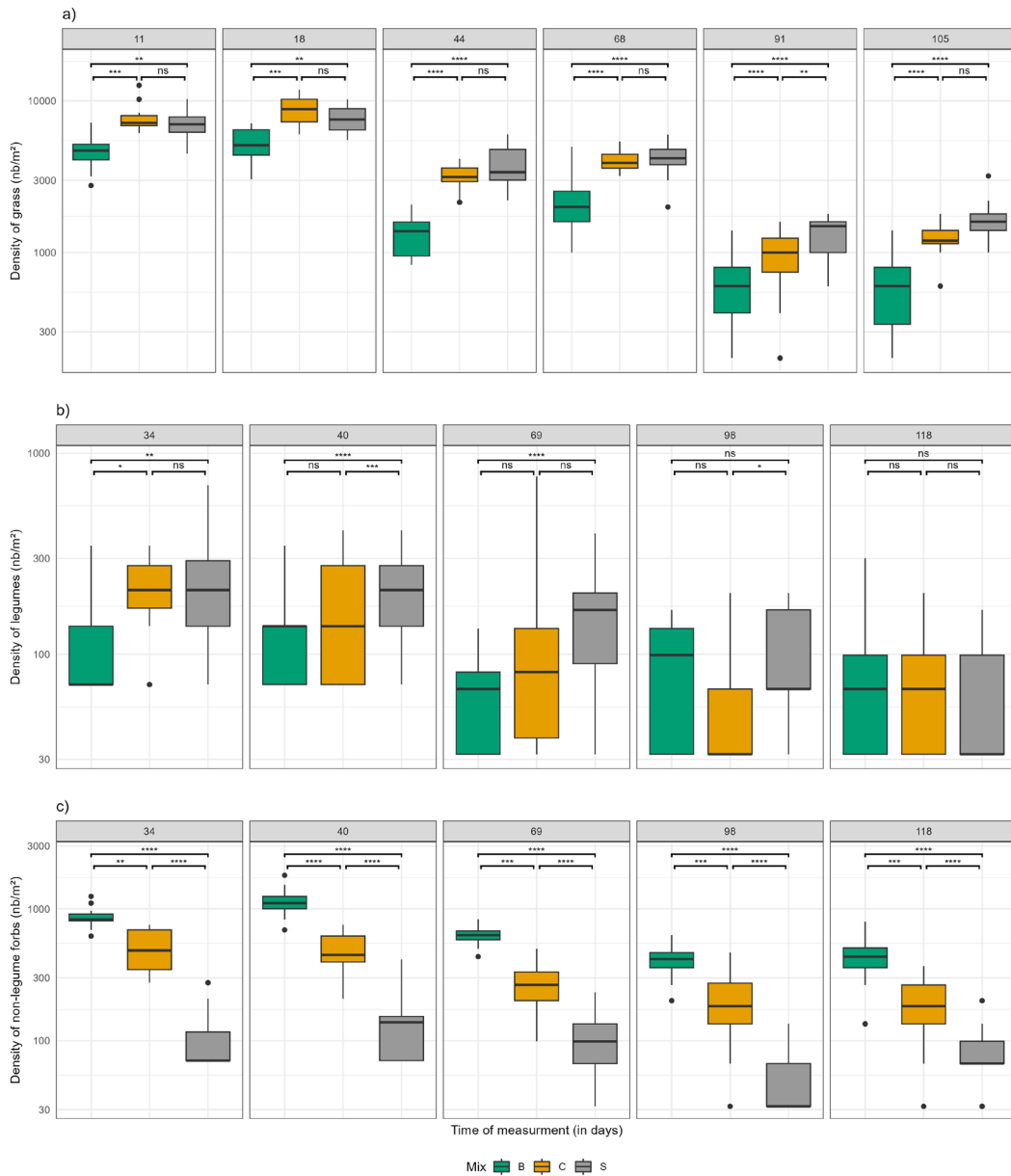
### Bloc

A slightly higher overall cover was found in GH ( $0.940 + -0.008$ ) compared with GC ( $0.964 + -0.005$ ,  $p = 0.006$ ) during the competition phase. No effect of the bloc was detected for the grasses or the legumes, but a significantly higher density of non-legume forbs was shown in GH ( $p = 0.02$ ). The effect of the bloc was especially present regarding the dry root biomass in the soil top-half, significantly higher in GC than in GH ( $p < 0.0001$ ).

## DISCUSSION

### Cover

Under the growing conditions of this experiment, the forbs produced individuals with very large leaf areas, certainly due to the absence of growth-limiting factors (abundant light, nutrients



**Figure 8.** Density of (a) grass, (b) legume and (c) non-legume forbs individuals per square meter in all three compositions. Symbols above indicate the level of significance for Tuckey comparisons among compositions: ns (non-significant), \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\* ( $p \leq 0.001$ ), \*\*\*\* ( $p \leq 0.0001$ )

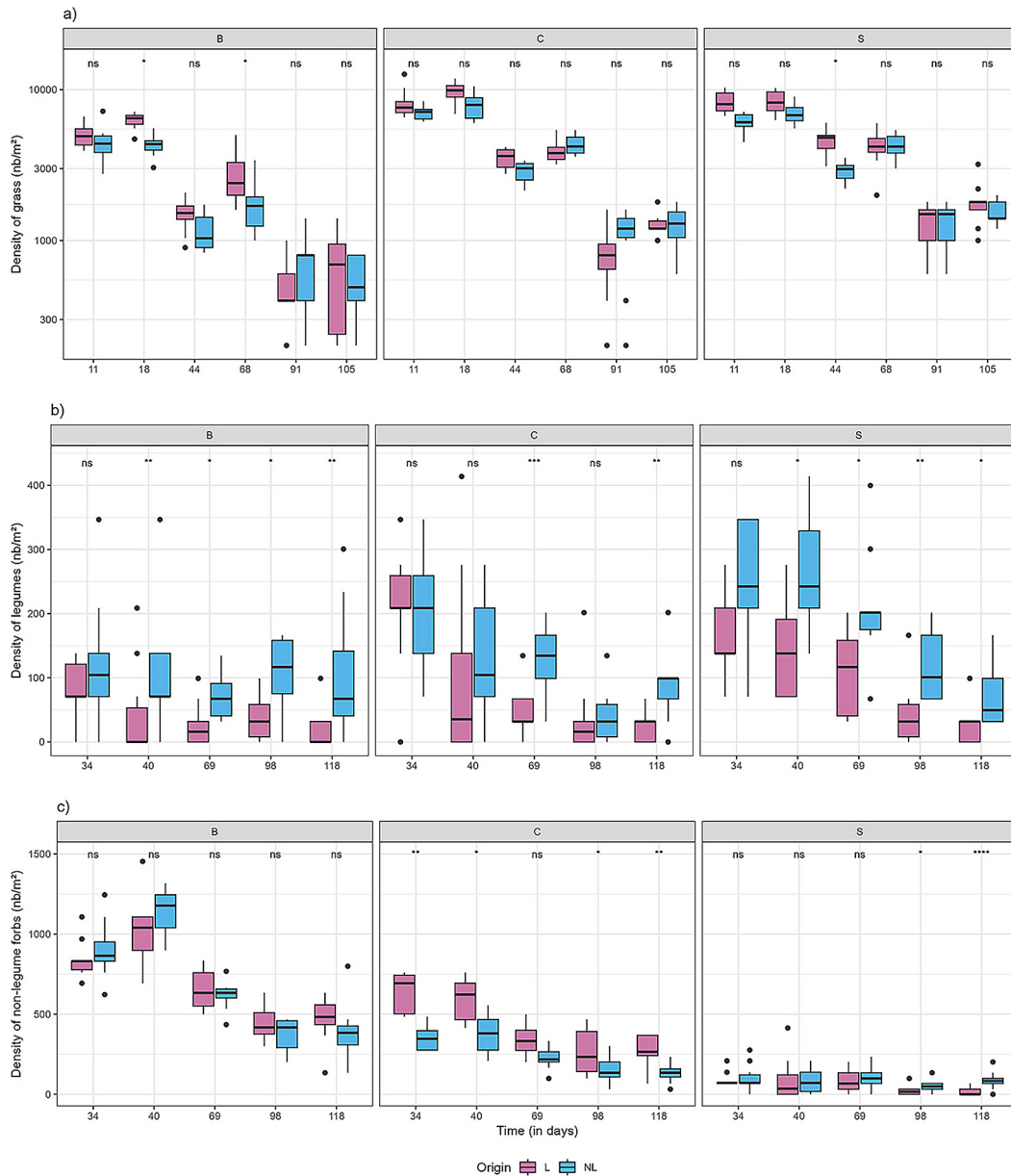
and water). This is probably why the Biodiversity mix, which contains more forbs, covered the ground more quickly than the other mixes. The loss of these large individuals during mortality inducing events may cause a direct deficit in cover.

The local origin resulted in a slower cover in the biodiversity composition during the growth phase, probably due to the smaller size of wild forbs individuals compared to cultivars, but a slightly better cover during the competition phase. Overall, the effect of the origin on cover is not clear enough in the conducted experiment to draw conclusions. Under difficult conditions, where resources are

limited and environmental stochasticity is high, the greater genetic diversity of local seeds, combined with a high species richness, could constitute a bet-hedging advantage because the probability of having a portion of species or genotypes resistant to these conditions is greater.

## Density

The difference in density of grass among compositions followed the expectations considering their relative proportion in seed weight. Regarding the effect of origin, it can be noticed that



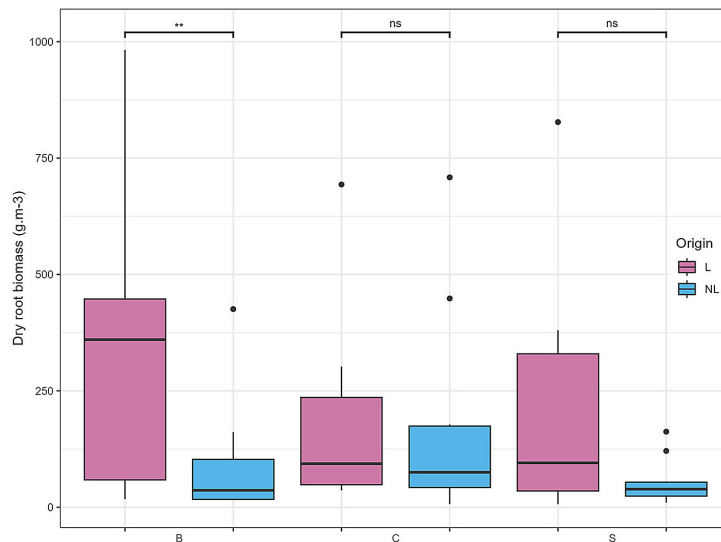
**Figure 9.** Density of (a) grass, (b) legume and (c) non-legume forbs individuals per square meter per origin in all three compositions. S, C, and B are for Standard, competitive, and biodiversity seed composition, respectively. NL and L are of non-local and local origins. Symbols indicate the level of significance for Tukey comparisons between origins: ns (non-significant), \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\* ( $p \leq 0.001$ ), \*\*\*\* ( $p \leq 0.0001$ )

the higher densities of grass in the locally sourced mixtures during the early period after sowing (day 11 to 44) suggests a better germination rate of local grasses. This goes against the expected advantage of cultivars under favorable controlled conditions because they are likely to have been selected for this by private breeders. Staab et al. [2015] also found a better establishment of “regional” seeds in the early period after sowing.

The densities of non-legume forbs observed in all three compositions were aligned with the seed content regarding species richness, relative

weight, and number of seeds (see Table 1 and Figure 2). The effect of the origin is not clear in the case of S and B. However, C-L had consistently higher densities of forbs than C-NL. It is possible that the wild and local variants of the few non-legume forbs present in the Competitive composition showed higher competitive differential than the rest of the species. Species-centered experiments would be necessary to answer these issues.

The densities of legumes observed were in line with the seed count of each composition (Figure 2). Across all three species compositions, the



**Figure 10.** Mass of dry roots (grams) per cubic meter in the topsoil. S, C, and B are for standard, competitive, and biodiversity seed composition, respectively. NL and L are of non-local and local origins. Symbols indicate the level of significance for Tukey comparisons between origins: ns (non-significant), \*\* ( $p \leq 0.01$ )

non-local origin returned higher densities than their local counterpart. Because of their widespread historical use in agriculture, the selection of characteristics providing a competitive advantage to Fabaceae cultivars might explain the higher densities observed across all three compositions.

Past the midpoint of the experiment and a few days after the end of the growth phase, the total density of plant individuals was very similar between S and C, but significantly lower in B. The quantity of seeds initially sown cannot explain this (Figure 2). The authors believe the higher cover observed during the entire growth phase and the presence of very covering forbs might have caused more mortality due to restricted access to light [Haynes, 1980]. The significantly higher total density in the local version of B is most likely linked to the higher density of grasses observed during the experiment.

### Roots biomass

The lower root biomass of the S composition might seem counterintuitive as the grasses are known to have a very dense and ramified root system in the top 20 cm of soil. However, grasses usually have finer and more ramified roots, providing a large exchange surface area but not contributing as much when evaluating root biomass following the adopted sampling protocol. The higher species richness present in both C and B might translate into more diverse root architecture

allowing for better exploitation of soil space and resources and reducing both intra and inter-specific competition. The likely higher genetic diversity in local seeds from the wild could lead to a greater variation of root morphologies. This can be an advantage in exploiting soil resources and in the ability to survive from one year to the next for perennial species.

The difference observed in the root biomass production between blocs corroborates the differential phenotypic response of the plant to the environment [Fitter, 2002]. Studies show the influence of air and soil temperature, delayed irrigation and available water on root growth, elongation and mass [McMichael and Burke, 1996]. The authors suspect the edge of local seeds regarding root biomass production might be further reinforced under changing and harsher edaphic conditions. In fact, when testing the model with the interaction of mix  $\times$  origin  $\times$  bloc, the local origin presented a clear advantage regarding root biomass production in the growing compartment (GC), where higher hydric stress occurred throughout the experiment due to irregularities in the manual watering process (Anaël Mayeur, personal observations). Accordingly, studies have shown adaptive responses of root system architecture and growth to environmental conditions. For instance, nutrient deprivation can lead to a stimulated root hair development, resulting in an improved aggregate stability on constructed slopes [Ola et al., 2015].



## Relations between cover and density

Density and cover are affected by multiple factors and influence each other, especially when competition processes occur. During the establishment phase, density is mainly influenced by the total number of sown seeds and the germination rate of every species, given that competition for access to resources is low. The total number of seeds depends on the relative proportion of each species in the mixture and the weight of thousand seeds (WTS) associated with each of them. The supplier informed the authors that the WTS of a species can also vary depending on its origin and selection process, with a rough estimate of 4% difference in favor of the cultivars (Figure 2d). It is possible that this difference has had some effect on the obtained density results. During this same phase, the evolution of cover depends on the density of plants as well as their size. The present study is part of a broader research project conducting multiple experiments both *ex situ* and *in situ* on road embankments. *In situ*, we were able to notice a great phenotypic variability between individuals of the same species, influencing both the quantity and size of the leaves (Anaël Mayeur, personal observations).

Once the carrying capacity of the milieu is reached, competition processes regulate populations sizes. The competition for soil nutrients and water can play a role but is most likely negligible under the growing conditions of the conducted experiment. The competition for underground space among the root systems might play a role in the survival of plant individuals. The access to light, highly dependent on vegetation cover, is most likely the major factor of influence on density and can be strongly influenced by plants morphological characteristics defining canopy height and architecture [Haynes, 1980]. Here lays the trade-off between cover and density: as less light is available, the mortality of individuals increases. Grasses are also well known for their high competitiveness regarding soil nutrients and water [Annicchiarico et al., 2014], hindering the development of forbs. During the experiment, grasses, which usually present more vertically oriented leaves under natural conditions, formed a dense carpet of leaves over the surface of the growing pots, effectively blocking the light for other species developing underneath. Therefore, a dominance of highly covering species might ultimately result in a lower richness overall.

## Implications for practitioners

As it was previously explained, the ability of a plant cover to reduce splash erosion depends on the morphological characteristics of the plant. The authors think that during the first years of colonization, and before grasses can form into tussocks, the more vertical orientation and low surface of their leaves may offer less of an obstacle to the falling raindrops. However, the high density of individuals may facilitate infiltration and add some roughness to the soil surface, thus retaining more sediments from water runoffs. Associating grasses with a diversity of other forbs could bring complementary functions regarding erosion control. The diversity of roots and canopy architectures in richer mixtures should allow for a better exploitation of soil and aerial resources, and act on a variety of erosion process including splash erosion, surface erosion and shallow mass movement. Indeed, it is already admitted that herbaceous vegetation contributes greatly to increase the soil shear strength and particles cohesion at the proximity of roots. The obtained results regarding cover during the growth phase and root biomass production are in line with the suggestion made by Fattet et al. [2011] that a variety of plant functional types in revegetation mixtures on slopes would result in a better ability to restrain surface erosion and superficial mass movement.

The expectations of practitioners regarding species diversity, functionality, the density of individuals and cover must be carefully assessed beforehand in regard of the local conditions of implantation and the objectives that are pursued. The present study mainly focuses on answering the geotechnical outcomes of different revegetation seed mixtures. One shall keep in mind the synergies and trade-offs with ecosystem functions and biodiversity-related services. For example, [Mola et al., 2011] show the antagonist relationship between vegetation cover and species richness linked to the early stages of ecological succession, suggesting that the dominance of a limited set of species might restrain the development of a richer community with more diversified functional traits. In any case, the authors believe that a bet-hedging strategy regarding the choice of seeds, including species and genetic diversity within species, is a good way to avoid technical failure and promote ecological functionality associated with revegetation operations. The success of revegetation operations can also depend

on the involvement of other ecological processes, like shown in [Bulot, 2023] regarding the role of engineer species (e.g. seed dispersing ants). The choice of adequate and functional revegetation mixes should in any case be complemented with an adequate engineering and treatment of the soils following some basic principles: (1) appropriately mold the slopes and redirect the water runoffs, (2) reduce soils compaction to support infiltration, (3) minimize exposure to chemicals to maintain plant survival and (4) create microrelief on landscaped areas [Forman, 2003].

## CONCLUSIONS

The relation between plant cover and erosion underlines the vulnerability or bare soils in the interval between the end of the landscaping operations and emphasizes the need for a prompt establishment of vegetation, either by spontaneous colonization or seeding operations. The use of native species for revegetation purpose is nowadays widespread among practitioner, to reduce the risk of introduction and compete with exogenous and potentially invasive species [Corbin and D'Antonio, 2004; Walker et al., 2015], and improve landscape integration [Federal Highway Administration, 2007a]. Reflections now go beyond and consider with a rising interest the use of wild and locally sourced seeds, betting on the co-evolution with other components of the ecosystems to favor biodiversity, the natural process of selection and the higher genetic diversity provided by this kind of material to anticipate the needs of adaptation to climate change [Rivière et al., 2022].

Despite conducting this experiment under controlled conditions supposed to favor conventional compositions and cultivars, no real disadvantage was observed in the use of species-diverse and wild and locally sourced seeds. These mixes even showed better performances regarding the early development of grasses and the overall production of root biomass. Further experiments are being conducted on road embankments, seeking to assess the geotechnical and ecological capabilities of these revegetation mixtures under field conditions.

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