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Contribution des espaces non cultivés à la biodiversification des agroécosystèmes méditerranéens via l'étude de la dispersion et la croissance de la végétation spontanée

Martin Faucher

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'INSTITUT AGRO MONTPELLIER

En Sciences de l'Eau

École doctorale GAIA – Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau
Portée par

Unité mixte de recherche LISAH

**Contribution des espaces non cultivés à la
biodiversification des agroécosystèmes méditerranéens
via l'étude de la dispersion et la croissance de la
végétation spontanée**

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Le 13 décembre 2024**

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Rapporteure

Rapporteure

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**UNIVERSITÉ
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Résumé

Le changement global, à la fois anthropique et climatique, représente une menace grandissante sur les agroécosystèmes et leur biodiversité associée. Afin d'augmenter leur résilience aux multiples pressions engendrées par le changement global, une solution consiste à augmenter la part de biodiversité végétale sauvage dans les infrastructures agro écologiques (IAE), à l'origine de nombreux services écosystémiques.

Dans ce contexte, le projet de thèse a visé à apporter des éléments de réponse concernant les effets des modes de production et des variables environnementales sur la circulation de la biodiversité végétale au sein des agroécosystèmes viticoles méditerranéens, à l'aide d'une approche combinant observation, expérimentation et modélisation. Le projet de thèse s'est intéressé aux interactions fines entre la biodiversité végétale et les flux d'eau sur trois processus clés: la structuration de la banque de graine du sol dans un milieu agricole marqué par un réseau hydrographique dense, la dispersion de la biodiversité végétale par hydrochorie, et la friction générée par la couverture végétale au sein des IAE ciblées.

L'observation menée sur la banque de graines du sol, reposant sur l'identification des espèces végétales ayant germé au sein d'échantillons de sols, a notamment mis en évidence une prévalence des graines dispersées par la faune au sein des fossés lorsque la part des IAE est importante, ainsi qu'une déplétion possible de la banque de graines le long d'un gradient de pente malgré la présence d'une couverture végétale.

Concernant l'hydrochorie, l'expérimentation à l'aide de graines marquées par fluorescence a montré l'importance de la couverture végétale des inter-rangs et du changement de rugosité associé dans la rétention des graines. Elle a également mis en évidence le biais potentiel à ne pas tenir compte de la forme des graines dispersées, les graines rondes étant plus sensibles à une variation du couvert végétal que les graines avec crochet ou plumets. Enfin, les observations et expérimentations ont permis d'alimenter MoVeGrowth, un modèle mécaniste simulant les flux d'eau et de graines traversant un couvert végétal. MoVeGrowth est à notre connaissance un des tout premiers modèles écohydrologique permettant une simulation journalière des interactions eau-végétation. L'exploration numérique de propriétés fonctionnelles du modèle, en l'occurrence l'impact du couvert végétal sur la rétention des graines et son effet de friction sur les écoulements a révélé une réduction potentielle de l'érosion des sols dans les inter-rangs de vigne, ainsi qu'une facilitation de la dispersion par hydrochorie au sein des fossés agricoles.

En conclusion, le travail de thèse a ré-interrogé la place de la végétation dans les agroécosystèmes méditerranéens pour lesquels l'eau, d'abord facteur limitant de la production végétale, est également structurante de la biodiversité végétale associée. Cette thèse plaide pour une meilleure connaissance des propriétés fonctionnelles de la végétation en lien avec les écoulements, afin de choisir des solutions fondées sur la nature, intégrant les pratiques d'entretien des IAE, qui maximisent la ressource en eau et la biodiversité.

Mots-clés : écohydrologie, agroécologie, solutions basées sur la nature, hydrochorie, traits fonctionnels, modèle mécaniste, banque de graines du sol

Abstract

Global change, both anthropogenic and climatic, represents a growing threat to agroecosystems and their associated biodiversity. In order to increase their resilience to the multiple pressures generated by global change, one solution is to increase the proportion of wild plant biodiversity in agro-ecological infrastructures (AEIs), which are the source of many ecosystem services.

Against this backdrop, the aim of the thesis project was to provide some answers concerning the effects of production methods and environmental variables on the circulation of plant biodiversity within Mediterranean wine-growing agroecosystems, using an approach combining observation, experimentation and modelling. The thesis project focused on the fine-grained interactions between plant biodiversity and water flows on three key processes: the structuring of the soil seed bank in an agricultural environment marked by a dense hydrographic network, the dispersion of plant biodiversity by hydrochory, and the friction generated by plant cover within targeted AEIs.

Observation of the soil seed bank, based on the identification of plant species that had germinated in soil samples, highlighted the prevalence of seeds dispersed by fauna within ditches when the proportion of AEIs was high, as well as a possible depletion of the seed bank along a slope gradient despite the presence of plant cover.

With regard to hydrochory, experiments using fluorescently-marked seeds demonstrated the importance of inter-row plant cover and the associated change in roughness in seed retention. It also highlighted the potential bias of ignoring the shape of dispersed seeds, round seeds being more sensitive to changes in plant cover than seeds with hooks or plumes. Finally, the observations and experiments were used to feed MoVeGrowth, a mechanistic model simulating the flow of water and seeds through a plant canopy. To our knowledge, MoVeGrowth is one of the very first ecohydrological models to simulate water-vegetation interactions on a daily basis. Numerical exploration of the model's functional properties, in this case the impact of plant cover on seed retention and its frictional effect on runoff, revealed a potential reduction in soil erosion in vineyard inter-rows, as well as a facilitation of dispersion by hydrochory within agricultural ditches.

In conclusion, the thesis work re-interrogated the place of vegetation in Mediterranean agroecosystems for which water, primarily a limiting factor in plant production, is also structuring the associated plant biodiversity. This thesis argues for a better understanding of the functional properties of vegetation in relation to runoff, in order to choose nature-based solutions, integrating AEI maintenance practices, that maximize water resources and biodiversity.

Keywords : ecohydrology, agroecology, nature-based solutions, hydrochory, functional traits, mechanistic model, soil seed bank

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Avant-propos

La biodiversification est une solution mise en avant pour augmenter la résilience des agroécosystèmes face au changement global (Dainese et al., 2019; Wezel et al., 2014), ce dernier étant défini comme la combinaison du changement climatique et des pressions anthropiques. Le concept de land sharing s'appuie sur la volonté de privilégier la végétation spontanée au sein des agroécosystèmes, afin de bénéficier d'une multitude de services écosystémiques au plus près des espèces cultivées (Fischer et al., 2014; Green et al., 2005). Dans la région méditerranéenne, une biodiversification locale via le land sharing permettrait de lutter contre l'érosion des sols et préserver la ressource en eau, deux enjeux majeurs qui menacent de s'aggraver dans les prochaines décennies (Busico et al., 2023; Mrabet et al., 2020; Santillán et al., 2020; Lagacherie et al., 2018).

Les fossés et les inter-rangs de vigne sont les éléments du paysage les plus susceptibles d'accueillir de la biodiversification locale. Densément répartis dans les agroécosystèmes viticoles méditerranéens, ces espaces sont régulièrement traversés par des flux d'eau lors des épisodes de pluie, et l'eau entre en interaction avec la biodiversité végétale, en dispersant les graines et en contribuant à leur germination. Il existe encore peu d'études sur les interactions duales entre eau et biodiversité végétale dans ce type de milieu, or une meilleure connaissance du fonctionnement écohydrologique des agroécosystèmes méditerranéens nous aidera à améliorer la résilience de ces milieux agricoles très anthropisés et sensibles au changement climatique.

Afin d'apporter des éléments de réponse sur le fonctionnement écohydrologique des inter-rangs et fossés agricoles en région méditerranéenne, j'ai mis en place une méthode de suivi de ces phénomènes complexes selon un continuum observation-expérimentation-simulation. Premièrement, j'ai échantillonné et caractérisé la banque de graines du sol pour mieux comprendre comment elle était structurée en fonction des pratiques et de leur localisation dans éléments du paysage (fossés et inter-rangs). Ensuite, j'ai mené une expérimentation pour comparer les capacités de déplacement des graines lors d'un épisode ruisselant naturel, en fonction des pratiques d'enherbement des inter-rangs de vigne. Les résultats issus des deux expérimentations ont ensuite été intégrés, avec nos connaissances issues de la littérature, dans un modèle mécaniste de croissance végétale simulant un couvert végétal au sein d'un espace non cultivé type, plus particulièrement un inter-rang de vigne ou un fossé. Ce modèle a été ensuite utilisé comme laboratoire virtuel pour tester l'impact du changement climatique sur les principaux services fournis par ces milieux, afin de pouvoir préconiser des changements de pratiques pour assurer la résilience des agro-écosystèmes méditerranéens au changement global.

Chapitre I. Introduction : contexte, état de l'art, et objectifs de la thèse

I. Contexte

1. Enjeux

Le changement climatique impacte directement et indirectement l'ensemble des biomes à des intensités variables. Il contribue à une réduction de la biodiversité, dont l'ampleur conduit un nombre croissant de chercheurs à la qualifier de 6ème extinction de masse (Wudu et al., 2023). Le bassin méditerranéen fait partie des zones géographiques les plus vulnérables à ces menaces (GIEC, 2022; Giorgi, 2006). En effet, il a été désigné comme un des "points chauds" du changement climatique par le Groupe Intergouvernemental des Experts du Climat (GIEC). Les experts estiment qu'il sera notamment marqué par des épisodes de sécheresse plus intenses et plus réguliers dans les prochaines décennies, tandis que les épisodes pluvieux seront plus rares (GIEC, 2022; del Pozo et al., 2019). Par ailleurs, le bassin méditerranéen abrite une part importante de la biodiversité mondiale, particulièrement vulnérable aux conséquences du changement climatique (Aurelle et al., 2022).

L'agriculture est une activité majeure au sein du bassin méditerranéen, qui se retrouve exposée à des pressions en raison du changement climatique. Comme la majorité de la surface agricole mondiale (Pimentel & Burgess, 2013), l'agriculture méditerranéenne souffre de l'érosion des sols (Paroissien et al., 2010). Dans cette région, l'érosion des sols est notamment liée à la réduction du couvert végétal, désherbé systématiquement par les agriculteurs car entrant en compétition hydrique avec la vigne. En outre, le désherbage systématique au sein des paysages agricoles a également causé une érosion de la biodiversité (Prosdocimi et al., 2016). L'augmentation prévue des températures et la diminution de la pluviométrie annuelle menacent d'aggraver ces phénomènes d'érosion (Busico et al., 2023; GIEC, 2022), et de sécheresse (Straffelini et al., 2024; Santillan et al., 2022).

2. Biodiversification

Pour se préparer aux conséquences du changement climatique en Méditerranée, une part grandissante de viticulteurs se tourne vers l'installation de systèmes d'irrigation pour leur vigne (van Leeuwen et al., 2019). Le passage à des variétés plus résistantes à la sécheresse est aussi une méthode en plein essor, quoique freinée en France par la législation encadrant les appellations d'origine contrôlée. Indépendamment de leur efficacité, ces méthodes n'impliquent pas une modification significative des pratiques culturales ayant contribué au changement climatique (Raven et Wagner, 2021). Pourtant, ces dernières sont aussi responsables de la baisse de la biodiversité (Dudley et Alexander, 2017), avec un impact négatif avéré sur la production agricole (Garibaldi et al., 2021; Cardinale et al., 2012).

En conséquence, l'utilisation de la biodiversité comme levier d'action face aux pressions du changement climatique offre la perspective de répondre au besoin de protéger les agrosystèmes viticoles en contribuant par la même occasion à réduire l'intensification agricole, elle-même cause majeure du changement climatique.

La diversification et l'enrichissement de la biodiversité dans les agrosystèmes ne peuvent pas se faire sans espaces non productifs dédiés. Deux philosophies sont souvent opposées dans la littérature, le land sharing et le land sparing (Fischer et al., 2014). Selon le concept de land sharing, ces espaces doivent se trouver au plus proche des surfaces cultivées, tandis que le land sparing représente la volonté de séparer les espaces productifs des espaces non productifs afin de pouvoir disposer de tous les moyens disponibles pour atteindre la finalité de ces deux espaces, c'est-à-dire le maintien de la biodiversité dans les espaces non productifs et la maximisation de la production agricole dans les espaces productifs (Fischer et al., 2014; Green et al., 2005). Plusieurs définitions des espaces non productifs existent, Holland et al. (2017) les définit comme "tout espace à l'intérieur ou à l'extérieur d'une parcelle accueillant une communauté végétale différente de celle cultivée".

Dans le cas précis des agroécosystèmes viticoles, Hall et al. (2020) considèrent qu'ils permettent de concilier land sparing et land sharing grâce à leur configuration alternant les espaces productifs et les espaces non productifs. En suivant la définition de Holland et al. (2017), tous les espaces non productifs limitrophes à la parcelle viticole peuvent être considérés pour le développement du land sharing. Le développement du land sharing pourrait donc prendre en compte les inter-rangs de vigne, ainsi que les tournières, et dans le cas des agroécosystèmes méditerranéens particulièrement, les fossés agricoles (Fig. I.1.).

De fait, la définition des espaces non productifs correspond à la définition des infrastructures agroécologiques (IAE) au cœur de nombreux projets de recherche (Vialatte et al., 2023). Les IAE sont définis comme des éléments non productifs du paysage ayant une influence directe sur la production agricole. Les IAE linéaires telles que les fossés agricoles et les inter-rangs de vigne ont souvent l'avantage supplémentaire de permettre une continuité écologique pour la biodiversité environnante parce qu'ils représentent des corridors utiles au déplacement et à la dispersion des espèces (Dollinger et al., 2015).

Les fossés agricoles sont des excavations anthropogéniques dont le rôle est la collecte et la conduite en dehors des parcelles de l'eau issue des épisodes de ruissellement de surface (Levvasseur et al., 2012), mais aussi de drainage (Carluer et Marsily, 2004), et le contrôle de l'érosion (Dollinger et al., 2015). Les fossés agricoles étant organisés en réseaux, ils sont connectés hydrologiquement et écologiquement, faisant d'eux des éléments cruciaux dans la santé des métacommunautés (Favre-Bac et al., 2014; 2017; Herzon et Helenius, 2008). La densité du réseau de fossés agricoles peut dépasser 200 mètres de fossé par hectare, avec toutefois une variabilité importante (Levvasseur et al., 2015). La plupart des fossés sont de simples excavations, mais certains peuvent parfois être revêtus par du béton. Dans le contexte méditerranéen, les fossés se caractérisent par l'intermittence de leur mise en eau à cause du climat méditerranéen. Ce dernier est marqué par des épisodes pluvieux rares et intenses, ayant lieu principalement en automne, avec une occurrence ponctuelle en hiver et au printemps.

Le fonctionnement écohydrologique des fossés est largement dépendant des pratiques d'entretien du couvert végétal. Ces pratiques consistent à retirer tout ou partie de la végétation vivante et morte. La majorité des pratiques sont mises en œuvre au moins une fois par an, notamment la fauche, le brûlis, et le désherbage chimique (Dollinger et al., 2015; Levvasseur et al., 2014). Enfin, le non-remplissage quasi-permanent des fossés agricoles méditerranéens les différencie des fossés nord-européens par une végétation terrestre plus abondante, faite de plantes herbacées et de buissons (Levvasseur et al., 2014), tandis que les fossés plus régulièrement en eau accueillent davantage de macrophytes (Blomqvist et al., 2003).

Les inter-rangs de vigne sont des linéaires encadrés par un ou deux rangs de vigne. La gestion de l'enherbement des inter-rangs de vigne a plusieurs objectifs : facilitation de l'entretien de la vigne, limitation de la compétition pour la ressource en eau avec la vigne, mais aussi réduction de l'apport de ressources aux ravageurs de la vigne (Garcia et al., 2018). Le labour, l'application d'herbicides, et la tonte sont les pratiques les plus répandues pour contrôler le

couvert végétal au sein des inter-rangs de vigne. La présence d'un couvert végétal au sein des inter-rangs de vigne n'est pas rare dans les régions viticoles tempérées, mais une couverture végétale peut aussi être observée dans des régions plus arides. En France en 2010, environ la moitié des vignobles étaient au moins en partie enherbés (Ambiaud, 2012).

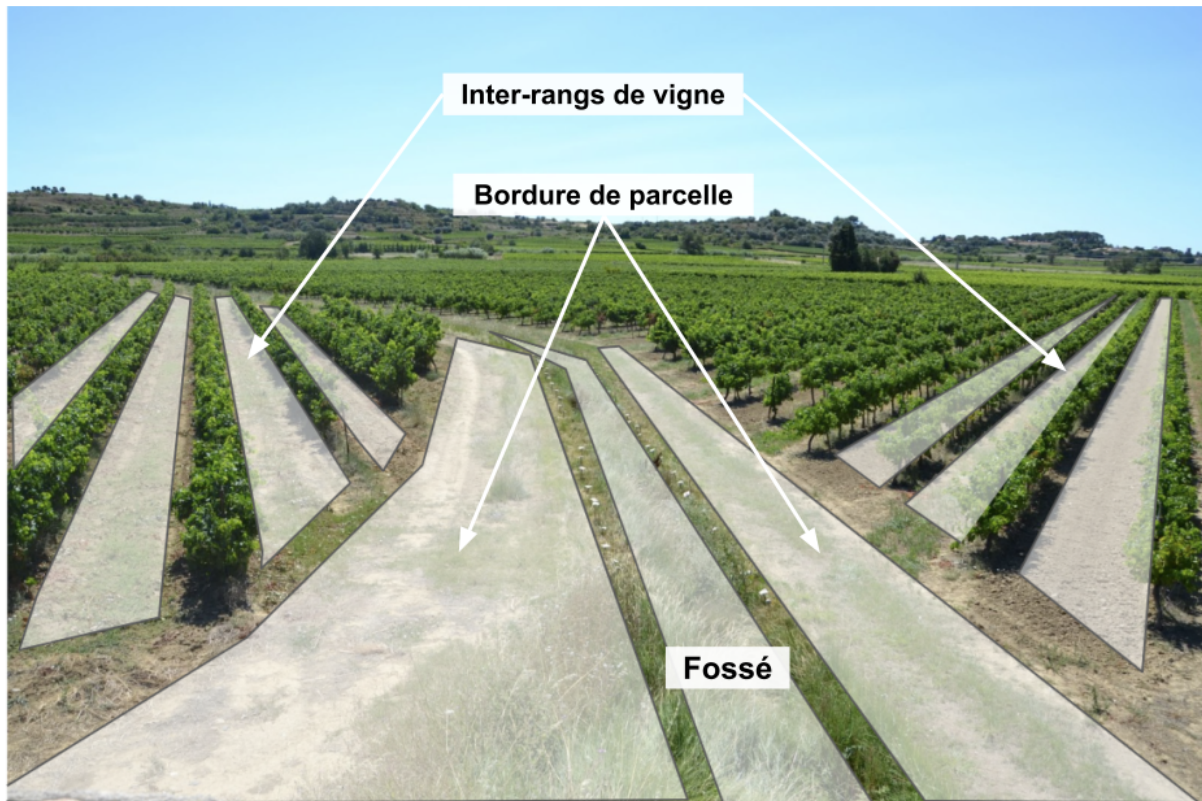


Figure I.1. Place des éléments interstitiels dans et autour d'une parcelle viticole méditerranéenne type

Les interactions entre l'eau et la végétation dans les infrastructures agroécologiques sont essentielles pour la durabilité et la résilience des systèmes agricoles. La végétation joue un rôle crucial dans la gestion de l'eau en captant et en retenant l'humidité du sol (Gaudin et al., 2010), ce qui réduit le ruissellement et l'érosion (Wu et al., 2020). L'écohydrologie est le domaine de recherche s'intéressant particulièrement à ces interactions, notamment leur résultat sur la répartition de la végétation au sein des cours d'eau (Rinaldo et al., 2018). Plus en détail, la friction générée par la végétation sur les écoulements d'eau a précédemment été étudiée dans les fossés méditerranéens (Rudi et al., 2022; 2018; Vinatier et al., 2024; 2017), ainsi que la capacité de rétention des graines au sein du couvert végétal (Rudi et al., 2021). Cependant la littérature est plus rare concernant ces mêmes interactions au sein des autres

IAE (inter-rangs) dont la fonction primaire n'est pas le recueil et la canalisation de l'eau (Merino-Martin et al., 2015).

3. Mise en place de la biodiversification : importance du continuum observation-expérimentation-simulation

La biodiversification suppose un apport de matériel biologique absent au démarrage du projet. Bien que cet apport puisse être exogène (Garrouj et al., 2024; Rydgren et al., 2010), il est préférable qu'il soit endogène, en s'appuyant sur la dispersion de la biodiversité existante (Sudduth et al., 2011). Cette dispersion peut être spatiale, mais elle peut aussi être temporelle dans le cas de la flore, par l'intermédiaire de la banque de graines du sol (Plue & Cousins, 2018).

La banque de graines du sol dans les agrosystèmes viticoles pourrait donc constituer une ressource importante de biodiversité végétale potentielle, dont la mobilisation ferait bénéficier la parcelle viticole de nombreux services écosystémiques (ex. réduction de l'érosion, augmentation de l'infiltrabilité du sol, lutte biologique contre les ravageurs, ...) (DeMalach et al., 2021; Plue et al., 2021). Toutefois la banque de graines du sol est une ressource difficilement estimable puisque cachée et située dans un volume de sol considérable (Mahé et al., 2021). Elle n'a jamais été estimée dans les milieux viticoles, et en particulier dans les IAE (inter-rangs et fossés). L'observation par échantillonnage est par conséquent indispensable pour obtenir une estimation de la biodiversité végétale potentielle à disposition des éventuels projets de biodiversification.

En amont de leur arrivée dans la banque de graines du sol, puis en aval lorsque les plantes issues des graines en produisent à leur tour, les graines sont dispersées plus ou moins loin de leur plante d'origine (Trep et al., 2021; Chen et al., 2020). La dispersion spatiale est par essence plus facilement observable, pourtant ses déterminants sont méconnus (Just et al., 2024). En plus d'étudier le réservoir potentiel de biodiversité végétale, comprendre les mécanismes déterminant la dispersion spatiale des graines est nécessaire pour caractériser la mise en place de la biodiversification. A ce titre, la mise en place d'une expérimentation facilitant le suivi des graines du début à la fin de leur dispersion par hydrochorie apparaît complémentaire à l'observation. En effet les expérimentations menées sur la dispersion des

graines par hydrochorie ont montré que l'immobilisation des graines à l'issue de leur dispersion n'était pas systématiquement suivie de leur germination dans les jours suivants (Chen et al., 2019; Rudi et al., 2018), ce qui les rend susceptible de rejoindre la banque de graines du sol (Nilsson et al., 2010, Fig. I.2.).

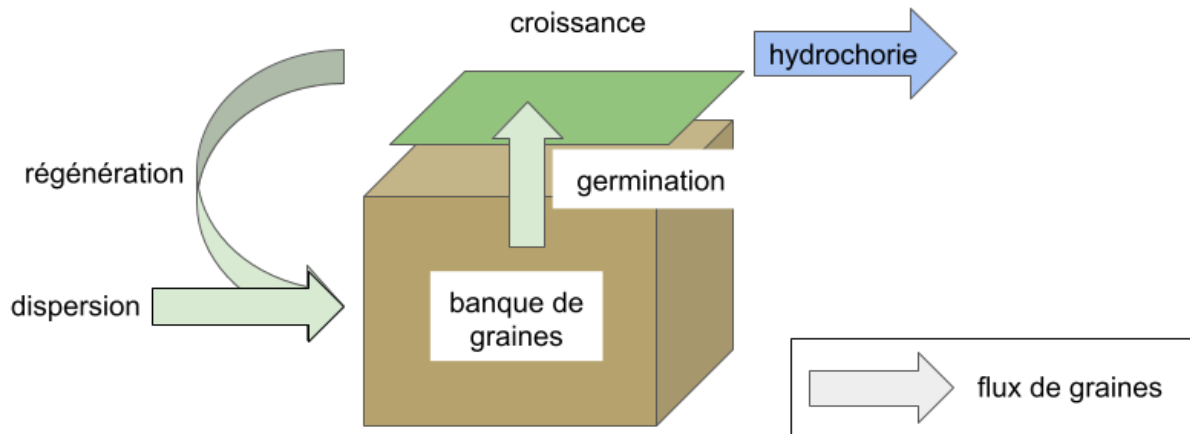


Figure I.2. Parcours d'un flux de graines du point de vue d'un ensemble surface-sol

Des connaissances concernant l'hydrochorie dans les fossés et lors de ruissellement de surface sont déjà disponibles (de Rouw et al., 2018; Rudi et al., 2018). De même, la friction générée par la végétation face à un écoulement d'eau a été estimée empiriquement (Rudi et al., 2021; Vinatier et al., 2018; 2017). En y additionnant les connaissances issues de l'observation de la banque de graines du sol et de l'expérimentation sur l'hydrochorie, le développement d'un modèle mécaniste simulant un couvert végétal permettrait d'explorer les effets cumulés de la végétation sur la friction et les écoulements d'eau, ainsi que les effets du changement climatique.

II. État de l'art

1. Banque de graines du sol

L'essor de la banque de graines du sol comme objet de recherche remonte aux années 1980, avec comme objectif initial de s'assurer que les adventices ne réapparaîtront pas après les opérations de désherbage. Dans une revue de la littérature regroupant les 60 articles portant sur la banque de graines du sol les plus cités 40 ans plus tard, Mahé et al. (2021) concluent effectivement que plus de la moitié d'entre eux se sont intéressés à la banque de graines du sol en tant que méthode de contrôle des pratiques.

L'idée d'utiliser le potentiel de la banque de graines du sol pour augmenter la biodiversité végétale d'un milieu a pris de l'ampleur au début des années 2000 (Bossuyt & Honnay, 2008; Bossuyt et al., 2002; Chang et al., 2001; Bakker et al., 1996). La banque de graines du sol a été identifiée comme cruciale pour le maintien de la diversité des communautés végétales (Plue & Cousins, 2018; Royo & Ristau, 2013). La fragmentation des paysages étant une des causes les plus fréquentes de baisse de qualité des milieux perturbés, la banque de graines présente l'avantage d'être moins pénalisée par les barrières à la dispersion (Plue & Cousins, 2013).

La détermination de la banque de graines doit permettre d'échantillonner un volume plus important qu'un relevé floristique, et ce à la recherche d'individus (i.e. les graines) de taille moins importante que les individus constituant la couverture végétale. En effet, la répartition des graines dans le sol peut être extrêmement hétérogène (Czarnecka, 2004; Caballero et al., 2003; Colbach et al., 2000; Ne'eman & Izhaki, 1999), à cause de taux de déplétion des graines différents (Meerts & Grommesch, 2001), d'une dispersion secondaire vers des zones d'accumulation de graines (Caballero et al., 2003), ou à cause du regroupement des graines autour de leur plante mère (Olano et al., 2005; Czarnecka, 2004). Selon Mahé et al., (2021), qui ont recensé la littérature existante sur le sujet, la quantité de sol échantillonnée ne semble pas dépendre d'un paramètre en particulier, mais plutôt de "la combinaison de différents paramètres tels que la taille de la parcelle, le nombre de parcelles étudiées et la main-d'oeuvre disponible." (traduit de l'anglais). Il n'existe à ce jour pas de méthode de détermination de la banque de graines véritablement dominante, deux grands types de

méthodes étant utilisés, parfois conjointement : la germination spontanée et l'énumération (Mahé et al., 2021).

Un protocole d'expérience de germination spontanée classique consiste à disposer les échantillons dans des bacs séparés mélangés à un terreau décontaminé, puis d'identifier les espèces présentes dans les échantillons au fur et à mesure que les graines qu'ils contiennent germent (ter Heerd et al., 1996). L'énumération implique de compter et d'identifier les graines, une fois filtrées et séparées de la matrice du sol, grâce à une loupe binoculaire. Cette dernière méthode est difficile à mettre en place dans le cas de sols cohésifs, en particulier les sols argileux tels que ceux occupant une part importante du littoral méditerranéen français.

2. Dispersion des graines par l'eau, ou hydrochorie

La dispersion des graines par de l'eau en mouvement, ou hydrochorie, a principalement été étudiée pour des espèces végétales aquatiques ou ripariennes, dans des plaines alluviales, des marais ou des cours d'eau permanents, artificiels ou naturels. Le terme d'hydrochorie peut s'appliquer au transport par l'eau de plusieurs unités végétales : les graines, des parties de la plante se détachant (ex : rhizomes, stolons, tubercules, ...), voire même la plante entière (Nilsson et al., 2010). Toutefois, la majorité des articles traitant d'hydrochorie se concentre sur le transport des graines.

Parolin (2005) recense trois formes d'hydrochorie : la nautochorie, qui concerne la dispersion à la surface de l'eau, la bythisochorie, qui concerne le déplacement par l'eau des graines en contact avec le sol (lit de rivière ou parcelles après des pluies importantes), et l'ombrochorie, qui concerne la dispersion liée à la séparation de la graine de sa plante mère causée par l'impact de la pluie (Nakanishi, 2002).

L'observation de la dispersion d'espèces végétales à travers un océan fait logiquement de l'hydrochorie le moyen de dispersion capable de déplacer les plantes sur les distances les plus longues (Cain et al., 2000), mais des observations dans la littérature semblent témoigner d'événements de dispersion longue distance impliquant de l'eau douce au moins supérieurs d'un ordre de grandeur à la distance maximale de dispersion par anémochorie (Sannikov et Sannikova, 2007). L'hydrochorie a pour avantages de déplacer les graines dans une seule direction et que la masse des graines ne soit potentiellement pas un problème. Dans les cours d'eau permanents, la dispersion par hydrochorie dépend des caractéristiques hydrologiques

du cours d'eau (Merritt et Wohl, 2002), des obstacles potentiels (ouvrages, bras de rivières, végétation, ...), et de leurs interactions (Rudi et al., 2018, 2020; Engström, Nilsson et Jansson, 2009).

Plusieurs articles indiquent que des espèces principalement dispersées par le vent (anémochorie) ou par fixation sur des animaux (épizoochorie) sont généralement bien dispersées par hydrochorie (Nilsson et al., 2010; Vogt et al., 2006), les appendices facilitant l'envol des graines ou les crochets permettant aux graines de se fixer sur les animaux augmentant la flottabilité des graines. Par ailleurs, l'hydrochorie se distingue des autres modes de dispersion par son rôle plus important de dispersion secondaire (Fig. I.3., de Werduwen et Ruxton, 2019). La dispersion secondaire désigne l'événement par lequel une graine ayant été dispersée une première fois est à nouveau dispersée grâce à un autre mode de dispersion que celui impliqué dans le premier événement.

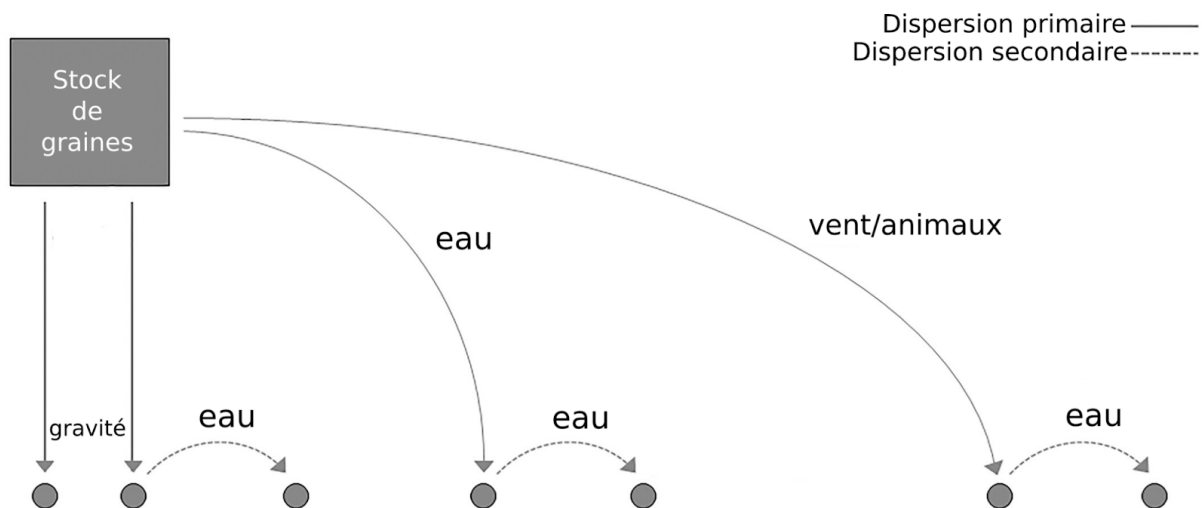


Figure I.3. Scénarios potentiels de dispersion de graines impliquant l'hydrochorie (dispersion par eau). Figure traduite et adaptée de Drees and Shea, 2024.

Une représentation de la dispersion par hydrochorie des graines mêlant des traits fonctionnels de la graine et différents modes d'écoulement de l'eau pour déterminer la facilité des graines à être dispersée a été conçue (Carthey et al., 2016). Selon cette représentation, les graines qui n'ont pas la flottabilité suffisante pour rester à la surface peuvent être transportées en suspension dans la colonne d'eau ou parmi les sédiments dans le lit du cours d'eau.

L'importance de la flottabilité pour l'hydrochorie dépend de la durée de la dispersion : si les graines sont dispersées par un événement hydrologique majeur, la force et la durée de cet événement rendent possible le déplacement de graines ne disposant pas d'adaptation particulière à l'hydrochorie, ce qui n'est pas le cas pour des temps de dispersion plus longs ou

lorsque l'hydrochorie succède à un autre mode de dispersion (Higgins et al., 2003). De plus, l'hydrochorie est parfois assimilée au transport sédimentaire dans les cours d'eau, une corrélation importante entre les sites de dépôt des sédiments et des graines ayant été observée à plusieurs reprises (Gurnell et al., 2006; 2008; Gurnell, 2007; Chambert & James, 2009), il est donc nécessaire ne pas uniquement prendre en compte la flottabilité.

Une méthode pour étudier l'hydrochorie sans se baser uniquement sur la flottabilité des graines est d'échantillonner les graines dispersées ou déposées dans un cours d'eau à l'aide d'un système de capture (Nilsson et al., 2010), ou de suivre le déplacement des graines grâce à un filin (Thomas et al., 2005), un étiquetage, ou un marquage (Zhang et al., 2022; Rudi et al., 2018; Kempter et al., 2018; Lemke et al., 2009; Fig. I.4). En contrepartie d'une récupération facilitée des données de dispersion, les méthodes de suivi nécessitant de manipuler individuellement les graines limitent les espèces pouvant être utilisées à celles disposant de graines suffisamment grandes pour permettre l'installation d'un tel dispositif, et sont difficilement compatibles avec le souhait de suivre un nombre important de graines, provenant d'espèces différentes. En comparaison, le marquage par une substance fluorescente ou réfléchissante peut être réalisé sur des volumes de graines importants, ce qui permet d'observer la dispersion d'espèces végétales produisant des graines de petite taille en grande quantité, ce qui est une caractéristique commune à beaucoup d'espèces végétales des paysages agricoles.

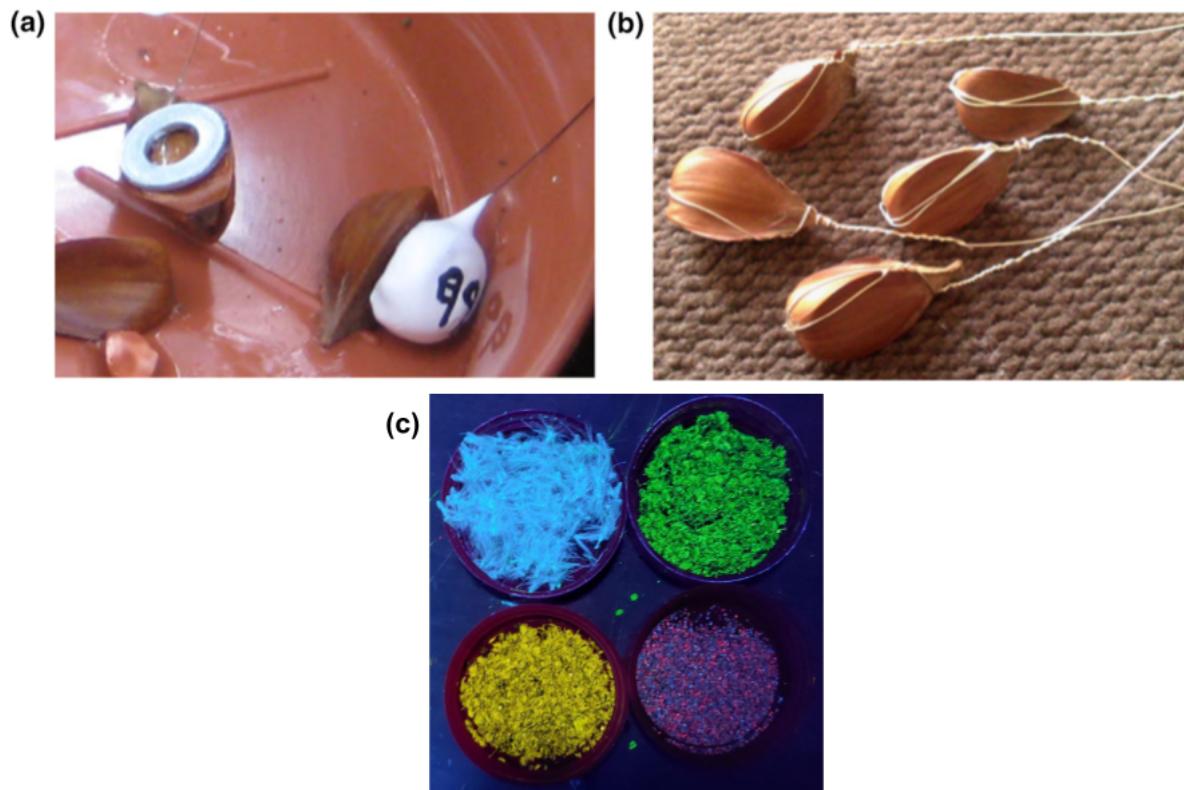


Figure I.4. Exemples de méthodes de suivi de graines : (a) Pièce métallique et colle (graine de gauche), émetteurs radio et colle (graine de droite), (b) bobine métallique, et (c) graines marquées par une poudre fluorescente à la lumière ultraviolet (UV), sous lumière UV. Sources : photographies (a) et (b), Kempter et al., 2018 ; photographie (c), Martin Faucher.

3. Modélisation de la croissance d'un couvert végétal et de la circulation de la biodiversité

La simulation fine de la croissance d'un couvert végétal a fait l'objet de nombreux modèles, principalement monospécifiques et basés sur des espèces cultivées. En France, le modèle STICS (Brisson et al., 2003) a été décliné et adapté à de nombreuses espèces (ex : pommier, Demestihis et al., 2018; riz, Courault et al., 2021; maïs, Jégo et al., 2011). Des modèles plurispécifiques existent aussi, permettant la modélisation d'association de cultures (Vézy et al., 2023; Malézieux et al., 2009), ou d'espèces adventices (modèle FlorSys, Colbach et al., 2020).

Divers modèles simulant une parcelle de vigne existent également (Sirsat et al., 2019; Moriondo et al., 2015; Cola et al., 2014), y compris développés à partir de STICS (Fraga et al., 2015; Valdes-Gomez et al., 2009). Plus spécifiquement, le modèle WaLIS a été développé dans le but de simuler le bilan hydrique d'une parcelle de vigne selon le niveau d'enherbement de ses inter-rangs (Fig. I.5, Celette et al., 2010).

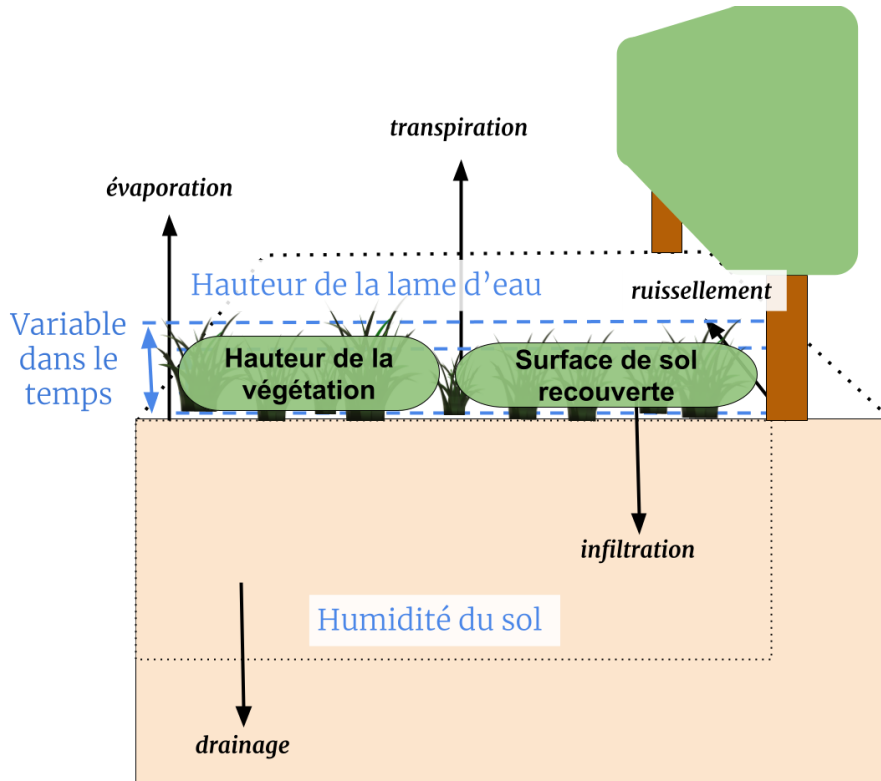


Figure I. 5. Représentation schématique du modèle WaLIS, adaptée de Celette et al., 2010

La modélisation de l'écoulement de l'eau au sein d'un milieu végétalisé a fait l'objet de nombreuses publications, principalement dans des cours d'eau permanents (Rudi et al., 2021; Nepf, 2012). Des modèles de fossés agricoles à l'immersion intermittente existent aussi, notamment pour modéliser la capacité de rétention de la végétation submergée pour la rétention de pesticides (modèle PITCH, Dagès et al., 2023) ou la capture de graines (Vinatier et al., 2017; Rudi et al., 2021).

Ces modèles de fossés agricoles reposent sur une utilisation de traits fonctionnels divergeant des utilisations typiquement rencontrées en écologie, notamment en écologie de la conservation (Munoz et al., 2023; Violle et al., 2017). Les traits fonctionnels sont définis comme les caractéristiques mesurables d'un individu impactant indirectement sa fitness à

travers leurs effets sur sa croissance, sa reproduction, et/ou sa survie (Violle et al., 2007). L'utilisation des traits fonctionnels en écohydrologie pour l'estimation de la perméabilité de la végétation aux particules et aux écoulements est plus rare, et constitue par conséquent un nouveau champ de recherches à explorer.

Enfin, la majorité de la modélisation de la dispersion des graines porte sur des travaux empiriques cherchant à extrapoler les distances de dispersion observées afin d'évaluer le potentiel dispersif (Kim et al., 2022; Bullock et al., 2017).

Le transport des graines par les animaux mis à part, la modélisation mécaniste de la dispersion par un facteur abiotique (i.e. l'eau ou le vent) apparente les graines à des particules inertes transportées par un flux turbulent (Thompson et al., 2014; Poggi et al., 2006). Cette approche a permis la simulation d'événements de dispersion au sein d'un couvert végétal homogène par le vent et des distances de dispersion associées (Nathan et al., 2002). Le modèle de Klausmeier est l'approche la plus commune pour traiter la question de la modélisation théorique de la dispersion des graines lors d'événements de ruissellement (Klausmeier, 1999). Le modèle assimile la dispersion anisotropique le long du gradient de pente à un mouvement d'advection équivalent à celui du flux d'eau (Consolo-Valenti et al., 2019). Néanmoins l'assimilation à des particules inertes freine la portée des résultats théoriques, puisque la capacité des graines à germer et à se développer est une composante fondamentale de l'étude de la dispersion (Nathan et al., 2002). Ces approches théoriques permettent toutefois de mettre en lumière la difficulté d'appréhender les événements de dispersion au-delà d'une certaine distance malgré les observations empiriques a posteriori de leur occurrence (Sannikov et Sannikova, 2007; Nathan et al., 2006, Fig. I.6).

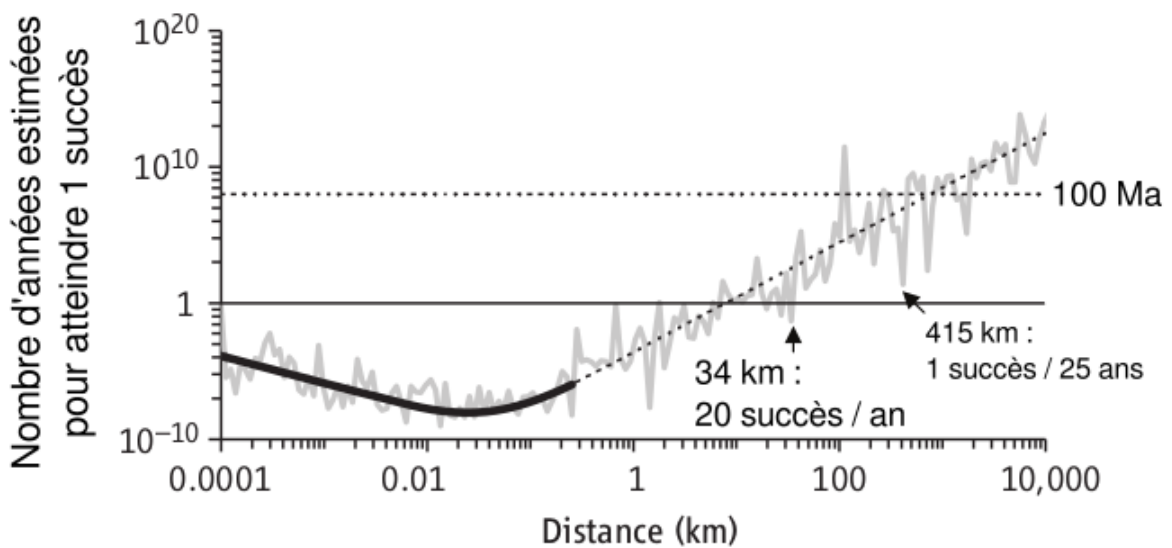


Figure I.6. Estimation du nombre d'années nécessaires pour atteindre 1 succès d'établissement d'une espèce à la suite d'un événement de dispersion, en fonction de la distance totale de dispersion. La ligne pointillée prolongeant la courbe en trait plein représente le point à partir duquel les méthodes actuelles permettent difficilement de quantifier des événements de dispersion à ces distances. Les flèches représentent la possibilité pour des événements théoriquement non observables de survenir. Figure extraite de Nathan, 2006.

Face à ces obstacles, la modélisation process-based est une démarche de modélisation s'attachant à reproduire un mécanisme par une méthode globale plutôt que par la formalisation d'un grand nombre d'éléments considérés comme nécessaires à sa réalisation. Cette approche a été mise en avant par Grimm au début des années 90 (Grimm, 1994; Grimm et al., 1996) avec comme point de départ le constat que les progrès de l'écologie en modélisation prédictive étaient entravés par trois obstacles : l'impossibilité de développer un modèle pour chaque région et chaque système, la méconnaissance du niveau de complexité suffisant pour obtenir des prédictions "utiles", et la constatation qu'à l'époque seuls des schémas simples observés à un seul niveau d'organisation avaient été étudiés (Grimm & Railsback, 2012). Grimm et Railsback proposent d'étudier les processus à petite échelle et les processus à large échelle ensemble plutôt que séparément, parce qu'ils sont interdépendants et que cette relation contient indirectement des informations sur ces processus. Cette approche a été utilisée avec succès dans des modèles d'écologie comportementale (Amano et al., 2006), d'écologie du paysage (Frair et al., 2008), d'écologie des populations (Lambert et

al., 2007; Piou et al., 2007) et des communautés (Muneepeerakul et al., 2008). Le cas particulier de la modélisation des cours d'eau en tant que corridors écologiques a été traité par une approche process-based (Rinaldo et al., 2018; Muneepeerakul et al., 2008).

III. Positionnement, zones d'étude de la thèse et objectifs

- 1. Positionnements scientifiques de la thèse

Circulation de la biodiversité végétale. La place centrale de la circulation de la biodiversité émane des conclusions des projets ayant eu l'objectif de se rapprocher d'un état non perturbé théorique ayant précédé la surface agricole. Deux questions émergent de ces projets, à savoir la définition de cet état originel, et la possibilité pour les espèces qui le composaient de recoloniser la surface ciblée. La première question est à l'origine de concepts tels que celui de naturalité, qui désigne la proximité d'un milieu sous influence anthropique à son équivalent "naturel" (Winter, 2012), ou celui d'hémérobie, qui évalue la tolérance d'une espèce végétale à la perturbation anthropique (Erdos et al., 2022). La détermination de ces deux termes étant imprécise, la recherche du milieu non perturbé n'a pas été traitée dans le projet de thèse, pour se concentrer sur la deuxième question. En plus de sa composition et de sa richesse, la biodiversité végétale sera donc étudiée à travers le prisme des graines qu'elle produit, ainsi que par l'intermédiaire de la friction qu'elle oppose aux flux qui la traversent. Le terme "circulation" englobe la dispersion spatiale des graines, mais aussi la dispersion temporelle que représente la banque de graines du sol. En y associant la modélisation de la croissance végétale, nous avons souhaité étudier plusieurs étapes clés du parcours d'une graine de sa création à sa germination potentielle, à une distance temporelle et spatiale plus ou moins importante de son lieu d'origine.

Services écosystémiques attendus. Ce travail de thèse s'est focalisé sur les déterminants de la fourniture de services écosystémiques au sein des inter-rangs de vigne et des fossés. La biodiversification de ces infrastructures agroécologiques repose en effet sur une compréhension accrue des processus à l'œuvre en leur sein, ainsi que leur évolution spatio-temporelle. Nous nous intéresserons essentiellement aux services dits de régulation et de maintenance, plus particulièrement au groupe de services dits de "régulation des flux

basaux et des événements extrêmes” tels que définis par le CICES (Common International Classification of Ecosystem Services) dans le cadre de la modélisation de la friction générée par un couvert végétal. L’étude de l’hydrochorie et de la banque de graines relèvent quant à elles du groupement de services dits de “soutien au cycle de vie et protection de l’habitat et du pool génétique”. Les services écosystémiques seront étudiés par l’intermédiaire de leurs fonctions associées, en aval de leur fourniture selon le concept de cascade des services écosystémiques (Fig. I.7, Potschin-Young et al., 2018).

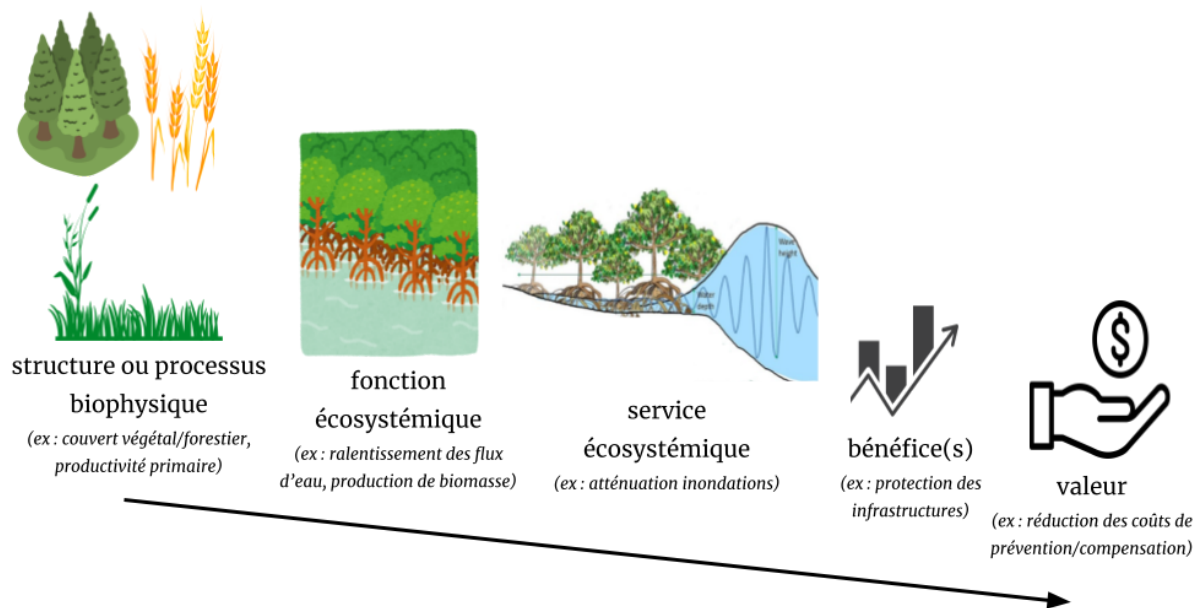


Figure I.7. Représentation du concept de “cascade de services écosystémiques” (Potschin-Young et al., 2018) à travers l’exemple de l’effet de la végétation sur l’atténuation des inondations

Interdisciplinarité. Selon la définition du métaprogramme Biosefair ayant financé une partie de ce travail de thèse, l’interdisciplinarité se définit comme : “l’interaction et la coopération de plusieurs disciplines de domaines différents autour d’objets et de projets communs”. Dans ce travail de thèse, l’écologie, l’hydrologie et la modélisation ont été simultanément sollicitées pour développer la compréhension des inter-rangs de vigne et des fossés. L’interdisciplinarité est à distinguer de la pluridisciplinarité, qui consiste en l’application d’une méthodologie provenant d’une discipline à la discipline cible du travail de recherche. L’interdisciplinarité est donc ici employée pour l’étude des inter-rangs de vigne et des fossés agricoles. Ces espaces non cultivés sont en effet à l’interface entre les transferts biotiques et

abiotiques, conditionnant par conséquent le fonctionnement écohydrologique du paysage agricole dans lequel ils s'inscrivent. En complément à l'écohydrologie, la modélisation intervient pour faciliter l'exploration de scénarios variés et permettre d'isoler un ou plusieurs facteurs pour étudier leurs effets.

Traits fonctionnels. Comme mentionné précédemment, l'utilisation de traits fonctionnels appliqués à l'écohydrologie constitue une originalité de ce travail de thèse. Lors de l'expérimentation sur l'hydrochorie par ruissellement de surface, les traits liés aux dimensions moyennes des graines utilisées ainsi que leur masse ont été mesurés afin d'obtenir des valeurs spécifiques de rapport masse/volume. Lors de la modélisation, la surface foliaire, la hauteur de la végétation, ainsi que la densité du couvert ont été utilisées afin d'estimer la résistance opposée par la végétation aux flux d'eau parcourant une parcelle viticole et le fossé agricole typiquement retrouvé sur son extrémité basse.

Choix de modélisation. Un point central dans une approche de modélisation est de trouver un point d'équilibre satisfaisant entre la complexité du modèle et son interprétabilité. Le modèle visant à rassembler les connaissances issues des expérimentations réalisées au cours du projet de thèse avec l'objectif de s'appuyer sur les traits de la végétation pour simuler la friction, la modélisation mécaniste de la croissance du couvert végétal sera favorisée face à la simulation hydrologique fine des écoulements d'eau.

- 2. Zones d'études

Ce travail de thèse a pris place au sein de deux zones d'étude situées en région méditerranéenne caractérisées par un climat similaire avec une pluviométrie annuelle comprise entre 600 et 750 mm. Ces zones se trouvent dans un paysage viticole sur un relief comparable, avec des pentes variant entre 5 et 15 % pour les deux parcelles viticoles contenues dans ces zones d'étude (Fig. I.8).

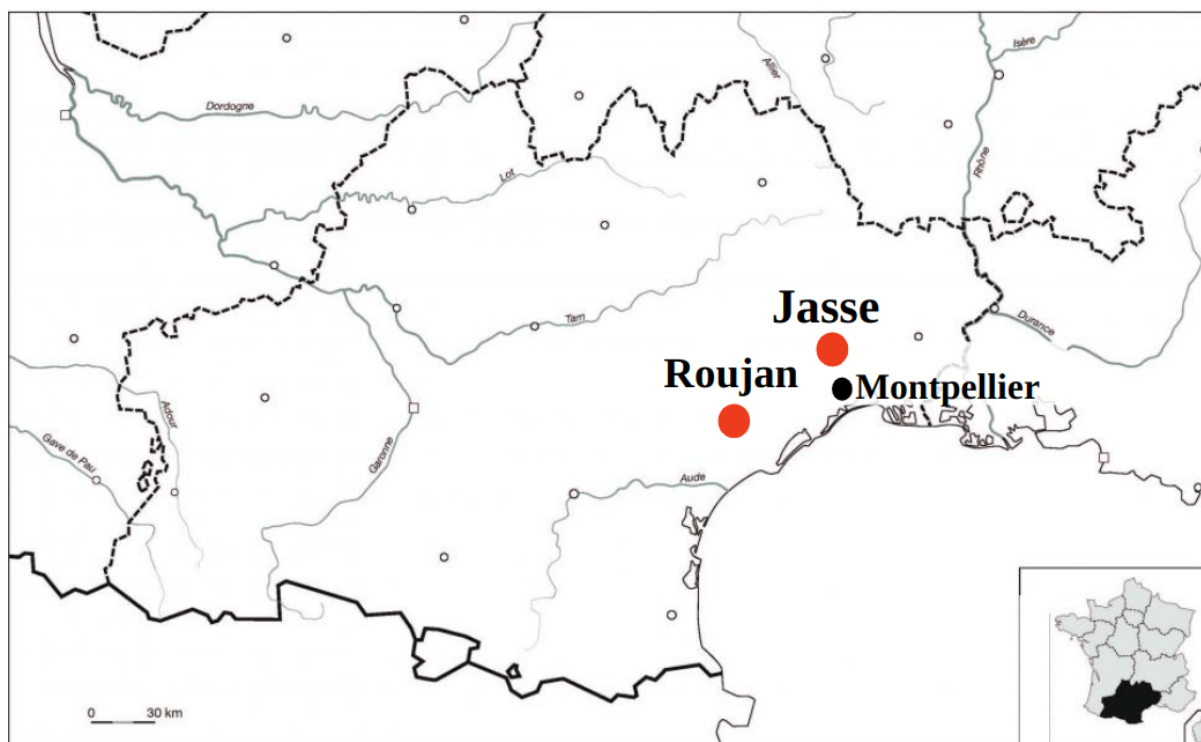


Figure I. 8. Zones d'études mobilisées au cours du travail de thèse

La zone d'étude de Roujan se situe dans le bassin versant de Roujan (34), suivi de longue date par l'UMR LISAH dans le cadre de l'ORE OMERE. Ce suivi implique la réalisation de relevés hydrologiques, pédologiques et agronomiques (Molénat et al., 2018). La zone d'étude s'inscrit dans un paysage agricole dominé par la viticulture, principalement conduite selon des pratiques agricoles conventionnelles. Au niveau paysager, ces pratiques conventionnelles ont favorisé un paysage simplifié, les éléments semi-naturels occupant 10% de la surface du sol située dans un rayon de 500m autour de la parcelle viticole (Fig. I.9a). Au niveau de la parcelle, ces pratiques conventionnelles s'expriment également par le désherbage systématique des inter-rangs de vigne (Fig. I9b).

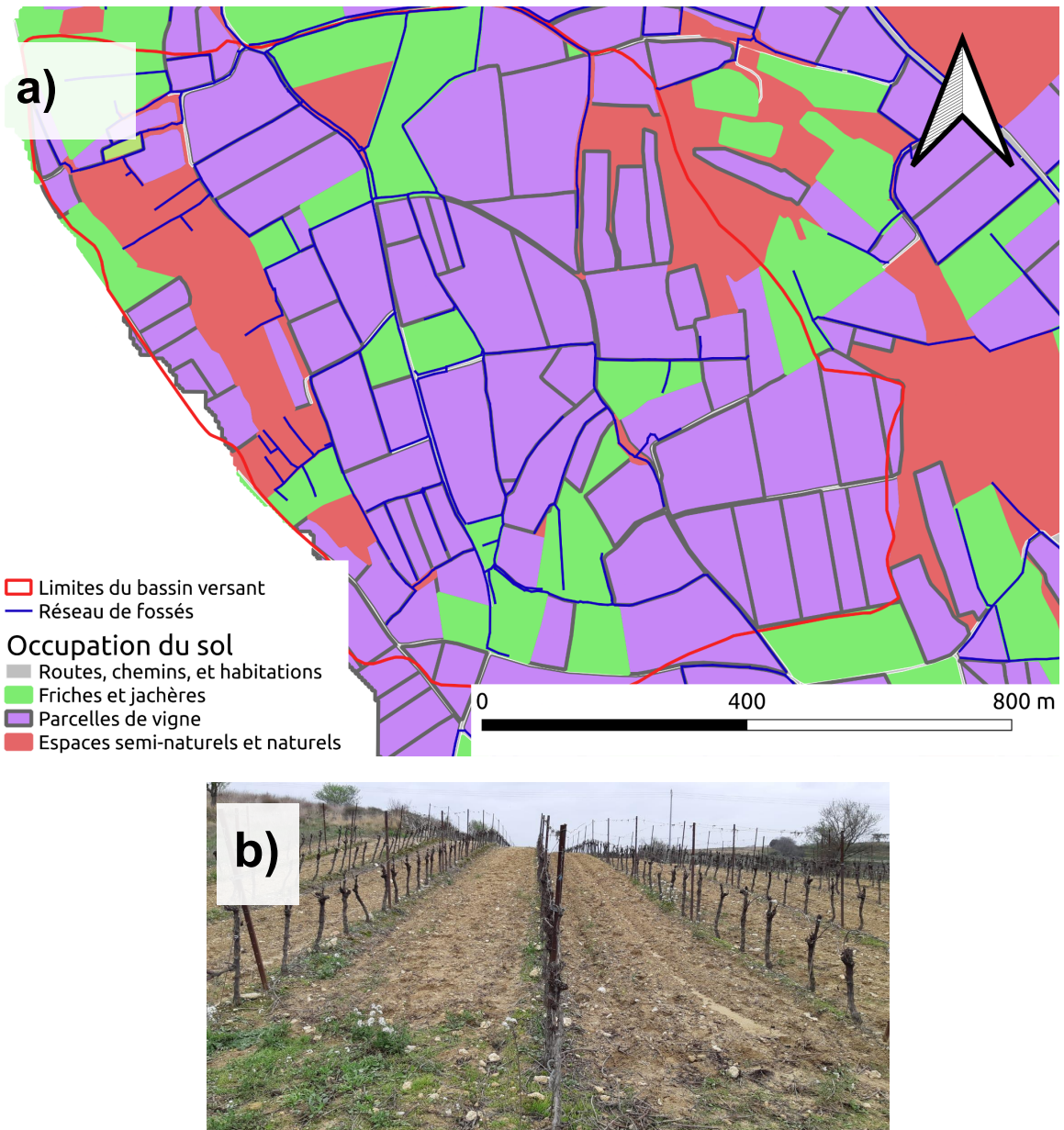


Figure I. 9. Occupation du sol au sein du bassin versant de Roujan (a), et enherbement au niveau de la parcelle étudiée (b).

La zone d'étude de la Jasse se situe au sein du domaine viticole de la Jasse, situé au nord de Montpellier. En lien avec la classification Haute Valorisation Environnementale (HVE) du domaine, le paysage dans lequel s'inscrit la zone d'étude est plus complexe que celui de la zone d'étude de Roujan. Ce paysage agricole complexe se traduit par des éléments semi-naturels occupant environ 40% de la surface de sol située dans un rayon de 500m de la parcelle viticole étudiée lors du travail de thèse (Fig. I.10). Au niveau de la parcelle, les

pratiques extensives associées à la classification HVE s'expriment par l'enherbement 1 rang sur 2 des inter-rangs de vigne (Fig. I.10b).

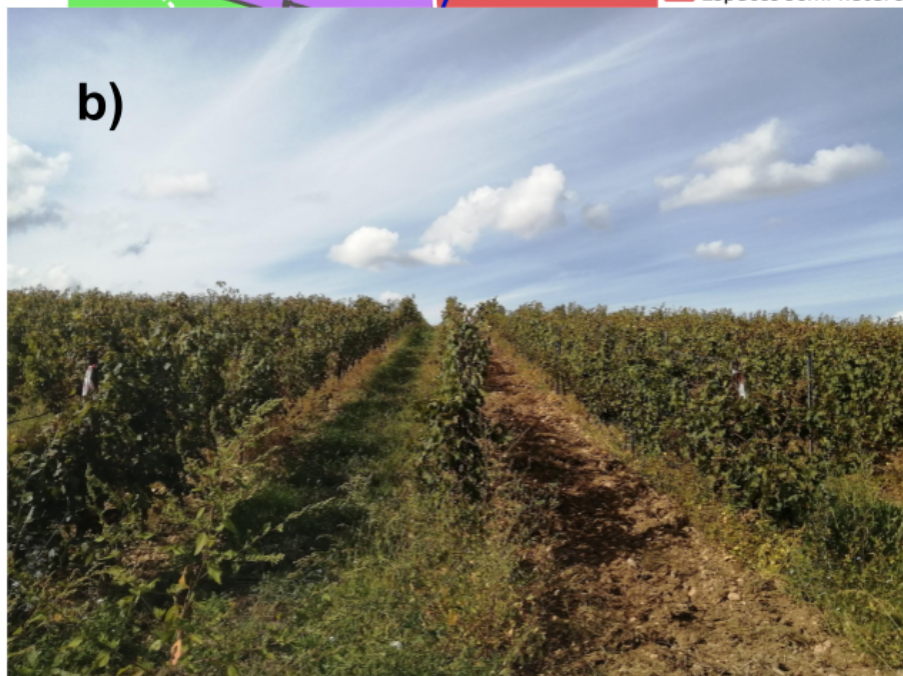
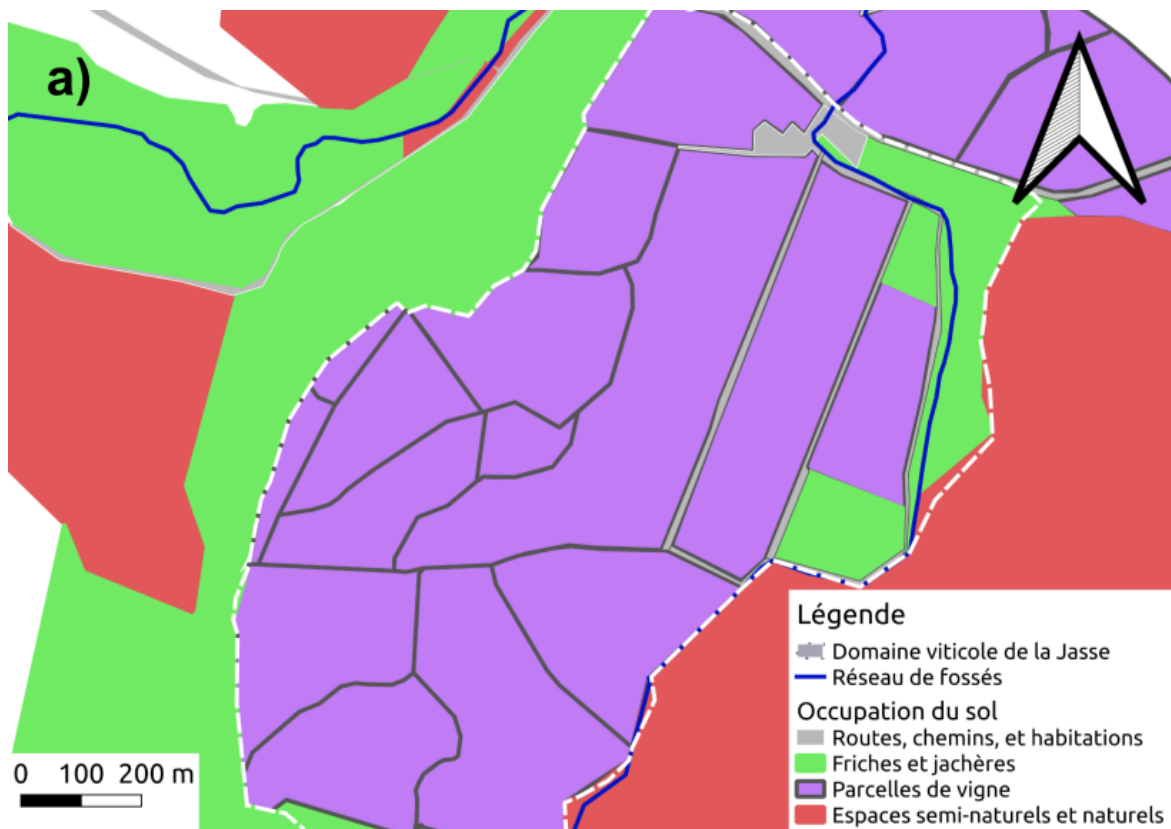


Figure I. 10. Occupation du sol au sein du domaine viticole de la Jasse (a), et enherbement des inter-rangs au niveau de la parcelle étudiée (b).

- III. 3. Objectifs scientifiques

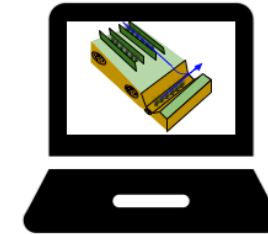
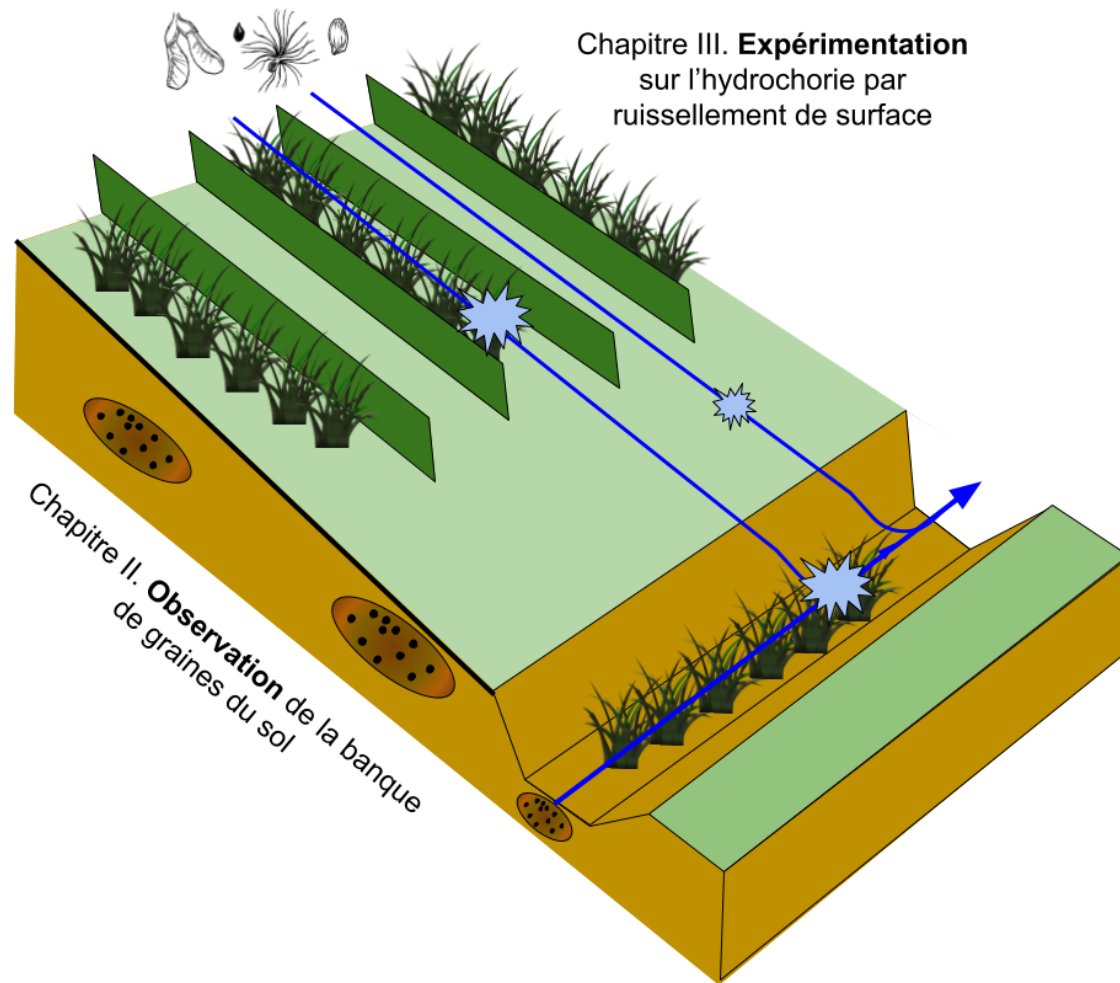
Les inter-rangs de vigne et les fossés agricoles sont des infrastructures agroécologiques essentielles dans la protection des agrosystèmes viticoles méditerranéens face aux conséquences actuelles et futures du changement climatique, mais aussi dans l'atténuation de l'empreinte environnementale de la viticulture. L'hypothèse centrale de ce travail de thèse est qu'il est possible d'atteindre une diversité spécifique satisfaisante dans un intervalle de temps réduit et à un coût minimal en s'appuyant sur les processus naturels de dispersion de la biodiversité végétale.

La thèse vise à répondre à la question suivante:

Quels rôles jouent les variables climatiques et les traits fonctionnels dans la circulation et le développement de la biodiversité végétale des agrosystèmes viticoles méditerranéens ?

La question principale de recherche se décline en sous-questions articulées selon 3 axes de recherche principaux, qui font chacun l'objet d'un chapitre dédié, rédigé sous la forme d'articles scientifiques ayant été soumis ou publiés au moment du dépôt du manuscrit :

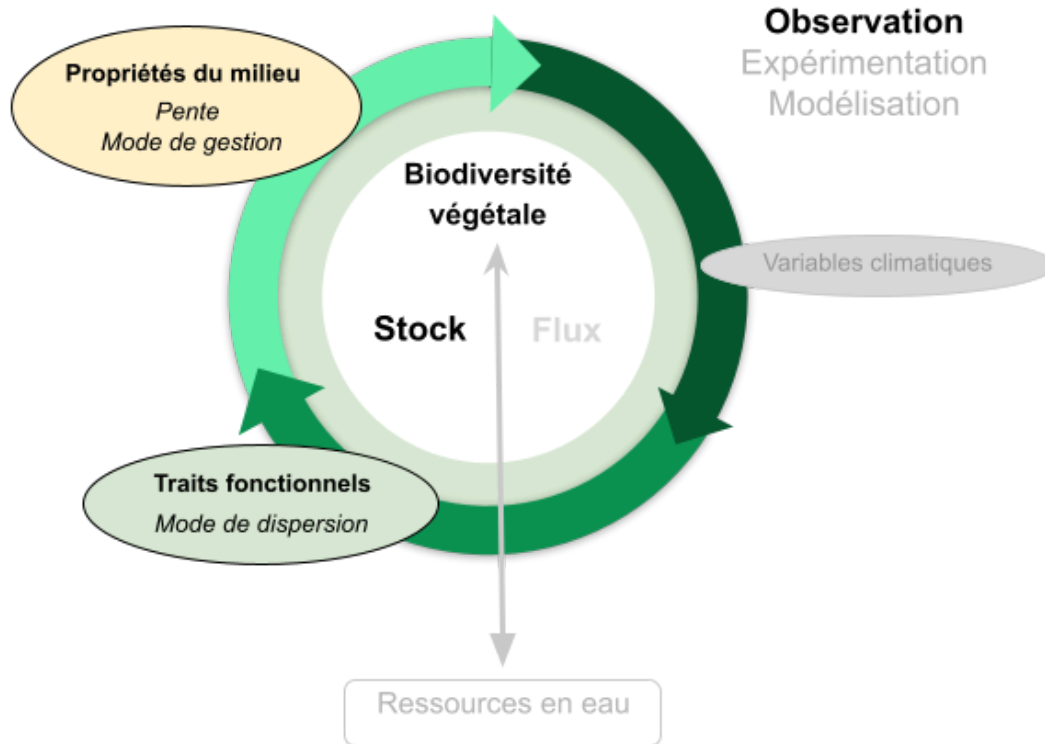
- **L'observation de la banque de graines du sol** a visé à obtenir des informations sur les effets de différents facteurs environnementaux sur l'approvisionnement et la déplétion des banques de graines des différents espaces non cultivés contenus au sein et autour d'une parcelle agricole méditerranéenne typique.
- L'approvisionnement et la déplétion de la banque de graines ont été associées à **l'expérimentation du potentiel de l'hydrochorie par le ruissellement de surface** observé dans les agroécosystèmes méditerranéens.
- La **modélisation de la végétation et de son effet sur les flux d'eau et de graines** a servi à explorer les trade-offs entre le niveau de végétalisation des espaces non cultivés et les flux d'eau et de graines par la comparaison des sorties issues de différentes combinaisons de scénarios climatiques



Chapitre IV.
Modélisation des
 flux d'eau et de
 graines

Figure I. 11. Représentation schématique de l'organisation du projet de thèse, et chapitres associés

Chapitre II. Observation de la banque de graines du sol



Ce chapitre porte sur la compréhension des différents facteurs pouvant influencer la banque de graines du sol retrouvée dans une parcelle viticole méditerranéenne et ses alentours directs. Plus spécifiquement, l'article s'est intéressé à l'influence de la pente, du couvert végétal ainsi que du mode de dispersion sur la diversité spécifique et la densité de la banque de graines du sol.

L'article qui suit a été publié dans la revue *Agriculture, Ecosystems and Environment* en 2024 sous le titre *Mediterranean vineyards seed bank characterisation along a slope/disturbance gradient : opportunities for land sharing*.

II. 1. Introduction

In the Mediterranean area, rainfall events are predicted to become more intense and droughts more severe due to climate change (Cozannet et al., 2022). In agrosystems, rainfall events will increase soil erosion caused by runoff, a phenomenon already considered problematic for more than three decades (Busico et al., 2023). Soil erosion causes multiple problems leading to a decrease in agricultural productivity (Pimentel & Burgess, 2013). A common practice to reduce erosion is to protect the soil with vegetation cover (Wu et al., 2020; Baraibar et al., 2021).

The presence of vegetation inside agrosystems would have additional benefits alongside erosion reduction. This idea is at the core of the concept of land sharing, which advocates for maintaining and/or increasing the surface of noncultivated zones found within agrosystems (i.e., hedgerows, field edges, ditches, etc.) (Green et al., 2005; Fischer et al., 2014). To be effective, land sharing requires a sufficient pool of plant biodiversity. This pool can originate from the biodiversity in adjacent habitats or directly from the soil seed bank (Erfanzadeh et al., 2010); thus, seeds can disperse through space or time (Plue and Cousins, 2018).

Using the soil seed bank to produce vegetation cover could be considered, but erosion has been associated with seed loss inside the field (Han et al., 2011; Janeau et al., 2022); thus, the potential of spontaneous vegetation cover could be threatened by the process it aims to reduce. Moreover, while the link between erosion and seed loss has been observed to be direct (García-Fayos, Bochet and Cerdà, 2010; Bochet, 2015), seed loss can also occur without erosion when light seeds are removed by runoff water whose force is otherwise too weak to displace soil particles (de Rouw et al., 2018); thus, vegetation cover may reduce erosion but not seed loss. To summarize, runoff can potentially reduce the potential of the soil seed bank to produce sufficient vegetation cover regardless of the surface state.

Most studies of the soil seed bank in agrosystems revolve around avoiding seeds from the soil seed bank from germinating to limit weeds in agrosystems (Mahé et al., 2021; Zhang et al., 2021; Adeux et al., 2023). There have been comparisons of the plant diversity between the field and its adjacent zones but those studies mostly investigated the aboveground vegetation (Fried et al., 2012; Minarro, 2012; Barrio et al., 2013; Holland et al., 2017; Cursach et al., 2020), and those that investigated the soil seed bank did not sample outside the cultivated

surface (Roschewitz et al., 2005; Fracchiolla et al., 2016; Carpio et al., 2020). Given the lack of linkability between the seed bank and the aboveground vegetation (Andreasen et al 2018), we need to confirm that the difference in diversity between the plot and its surroundings is also found in the seed bank.

Together with the field edges, the soil seed bank of agricultural ditches is also not well known. While plant communities inside ditches have been studied (Blomqvist et al., 2006), recent observations of the soil seed bank are lacking. However, ditches are interesting from a restoration perspective because they act as ecological corridors (Herzon and Helenius, 2008; Dollinger et al., 2015); thus, they can accelerate spatial dispersal and improve soil seed bank diversity.

Most spatial dispersal modes can be grouped into four main vectors: wind (anemochory), water (hydrochory), animals (zoochory), and gravity (barochory). Usually, spatially dispersed seeds become a part of the soil seed bank (Dekker, 1999), but the relative contribution of the different dispersal syndromes to soil seed bank replenishment is still unclear (Benvenuti, 2007). Therefore, studying the soil seed bank could also provide information on the potential plant community and the impact of different dispersal modes on soil seed bank replenishment.

To evaluate the potential of vegetation to reduce seed loss and the effect of practices and dispersal modes on the soil seed bank, we set up an experiment to determine the soil seed bank distribution within two Mediterranean vineyards and their adjacent environments, namely, their respective field edges and bordering ditches. The soil seed bank was then described in terms of seed density and species diversity at each sampled point. We formulated three main hypotheses: (1) The effect of the slope on the soil seed bank will be different between tilled and vegetated interrows. We also expect (2) operations within the field to deplete the soil seed bank; thus, the soil seed bank will be denser and more diverse in the field edges and the ditches than within the field. Grouping species into anemochory, hydrochory, barochory, and zoochory, we expect that (3) the effect of slope or position in the study site on the soil seed bank will be different depending on the dispersal mode.

II. 2. Materials and methods

2.1. Study sites

Two study sites in the Hérault Department (France) were selected for the experiment (Fig. II. 1).

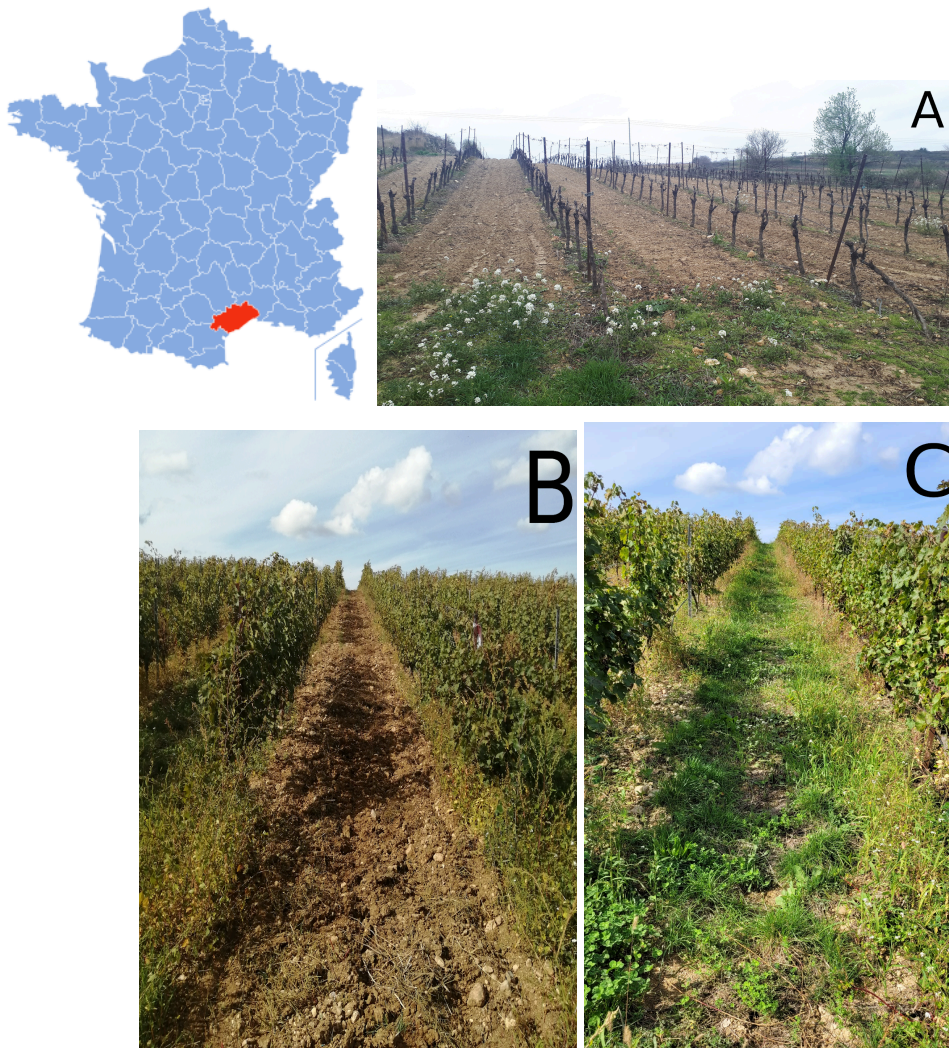


Figure II. 1. Location of study sites and visualization of interrows in the Roujan study site (A) and the tilled (B) and vegetated (C) interrows of the Combaillaux study site

The first study site, herein designated as the P1, is in the Roujan catchment ($43^{\circ}30'N$, $3^{\circ}19'E$), situated west of Montpellier, France. The Roujan catchment has been monitored since 1992 as a part of the long-term observatory ORE-OMERE (Molénat et al., 2018). The Roujan catchment area is a small catchment area ($<1 \text{ km}^2$) mainly occupied by vineyards

framed by a network of drainage ditches dug by farmers to drain some of the water from the soil, collect runoff and limit erosion. The catchment is characterized by a sub-Mediterranean subhumid climate with a long dry period, and the majority of rainfall occurs in spring and autumn. The average rainfall is 600 mm.year⁻¹ (Molénat et al., 2018). The vineyards that constitute most of the Roujan catchment area belong to different producers. The maintenance of the drainage ditches is the responsibility of the owners of the vineyards they cross and typically consists of removing the vegetation by mowing or burning the vegetation to preserve the water flow capacity. More rarely, dredging/chemical weeding operations are carried out. Within the Roujan catchment, P1 is a vineyard of approximately 0.3 ha of Pinot Noir grape variety planted on Calcaric Regosols with a mean slope of approximately 15%. Rows are oriented from east to west. The vineyard is bordered by other vineyards and a drainage ditch located downstream of the most sloping part of the vineyard. All interrows of P1 are chemically weeded, and the calendar of practices has not changed in the last 5 years before the sampling took place. When sampling took place, P1 was dominated by Poaceae and Brassicaceae in the field and the field edge, and by *Rubus fruticosus* inside the ditch.

The second study site, referred to as the P2, is in a vineyard situated north of Montpellier in Combaillaux (UTM 43.659903, 3.767451, first sampled interrow). The climate there is also classified as Mediterranean and subhumid, with an average rainfall of approximately 760 mm.year⁻¹. The vineyard is HVE-certified (Haute Valeur Environnementale - High Environmental Value), which requires a low use of synthetic chemical inputs, a significant share of vegetated interrows, and a share of diversified noncultivated zones situated above a threshold value. P2 has a surface area of approximately 3 ha of Merlot grape variety, clay-limestone soil, and a mean slope of approximately 20%. Similar to the P1, rows are oriented from east to west. An agricultural ditch downstream of the vineyard collects run-off water. This ditch separates the vineyard from another field left fallow for part of the year and sowed the remaining time. In this adjacent field, faba beans were sown during soil seed bank sampling. Every second row is mown and plowed after the harvest and then sown, and the remaining rows are simply mown. When sampling occurred, P2 was dominated by a mix of Fabaceae and Poaceae, and the ditch was mostly composed of *Rubus fruticosus* and *Clematis vitalba*. After sampling in April 2022, a *Trifolium* mixture was sown, and the faba bean seedlings produced by the adjoining land were sown in September 2022.

As the soil seed bank could be influenced by its surrounding areas, we estimated landscape diversity inside a 500-m radius buffer around the study site following the methodology from

Carpio et al. (2020). We classified orthoimages from 2021 (source: IGN) in vineyards, other agricultural land and seminatural habitats to obtain the surface proportion of each land cover. We digitized surrounding fields mainly composed of agricultural ditches to obtain a cumulative linear length inside the radius. Consequently, P1 is primarily composed of other vineyards (approximately 70%) and other agricultural lands (approximately 20%), with a small amount of seminatural habitats (approximately 10%). The buffer encompasses more than 8 km of agricultural ditches. P2 is composed of vineyards (approximately 55%) and seminatural habitats (approximately 40%). The buffer encompasses approximately 3 km of agricultural ditches.

Soil analyses were conducted at both study sites on soil samples taken alongside the soil seed bank samples. Samples were analyzed for pH, total carbon and nitrogen, organic matter content, cation exchange capacity, and concentrations of P, Mg and Na. Data were ultimately removed from the analysis due to a lack of significant results (Appendix A).

2.2. Soil seed bank sampling protocol

Soil seed bank sampling was carried out along a 50-meter transect consisting of 8 points starting upslope within the field until the ditch at the bottom of the study site. The first four sampling points are situated within the field, with T1 at the top of the slope and T4 at the bottom of the slope. Sampling was carried out using a corer that allowed the sampling of 10 cm diameter cylinders at a depth of 10 cm. The number of interrows sampled was determined so we had at least 3 interrows with the same vegetation state. For each point, 4 samples were collected. In the P1, 3 interrows were sampled with a spacing of one interrow between each of them (Fig. II.2). The first row of the vineyard was not sampled to avoid edge effects. In total, the sampling area covered approximately 350 m²

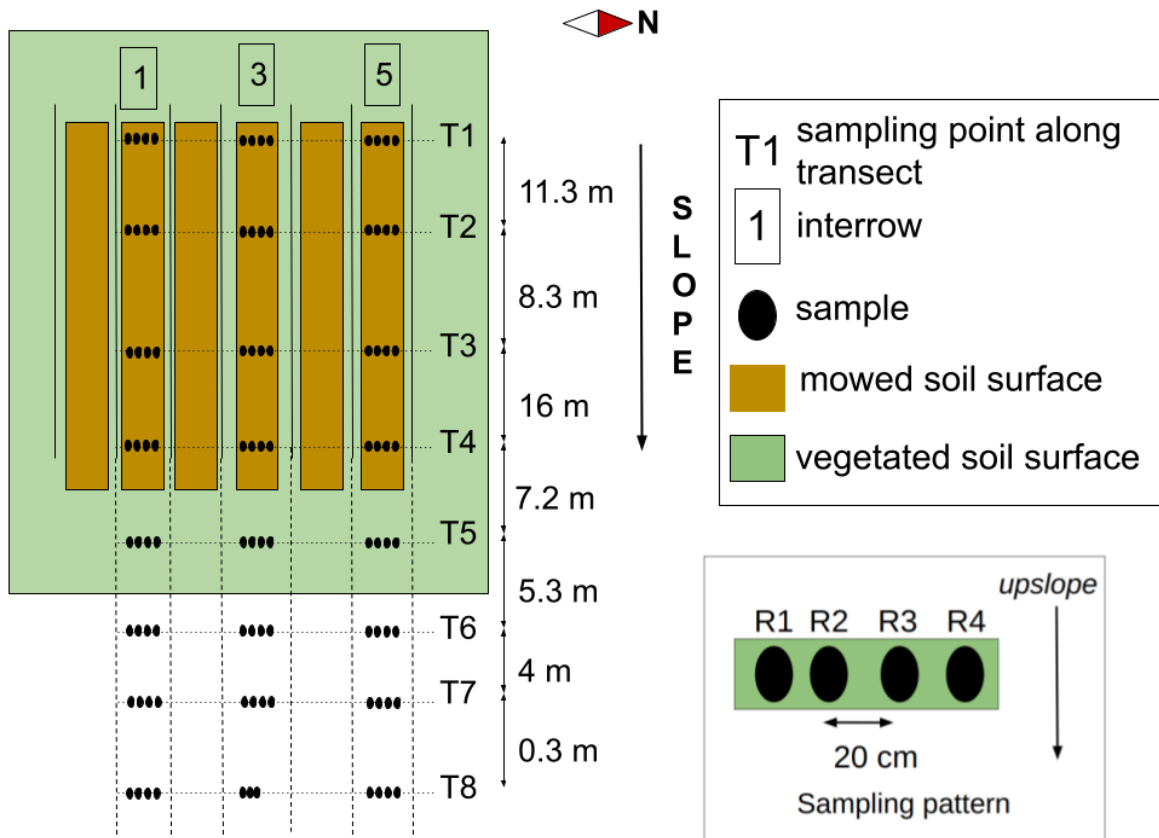


Figure II. 2. Representation of the Roujan vineyard (P1) and sample distribution. Each sample point represents 4 samples taken on a straight line approximately 20 cm from each other.

In the P2, 6 interrows were sampled, one with permanent plant cover and the other plowed after harvest (around mid-September) and then sown in April 2022. The sampling area covered approximately 2000 m² (Fig. II.3).

In total, 286 soil samples were collected for the soil seed bank of the two study sites, representing 9 interrows, 8 sampling points and 4 replicates at each sampling point, except one in the P1, where we were only able to collect 2 soil samples because the soil layer was too thin to collect the other two samples.

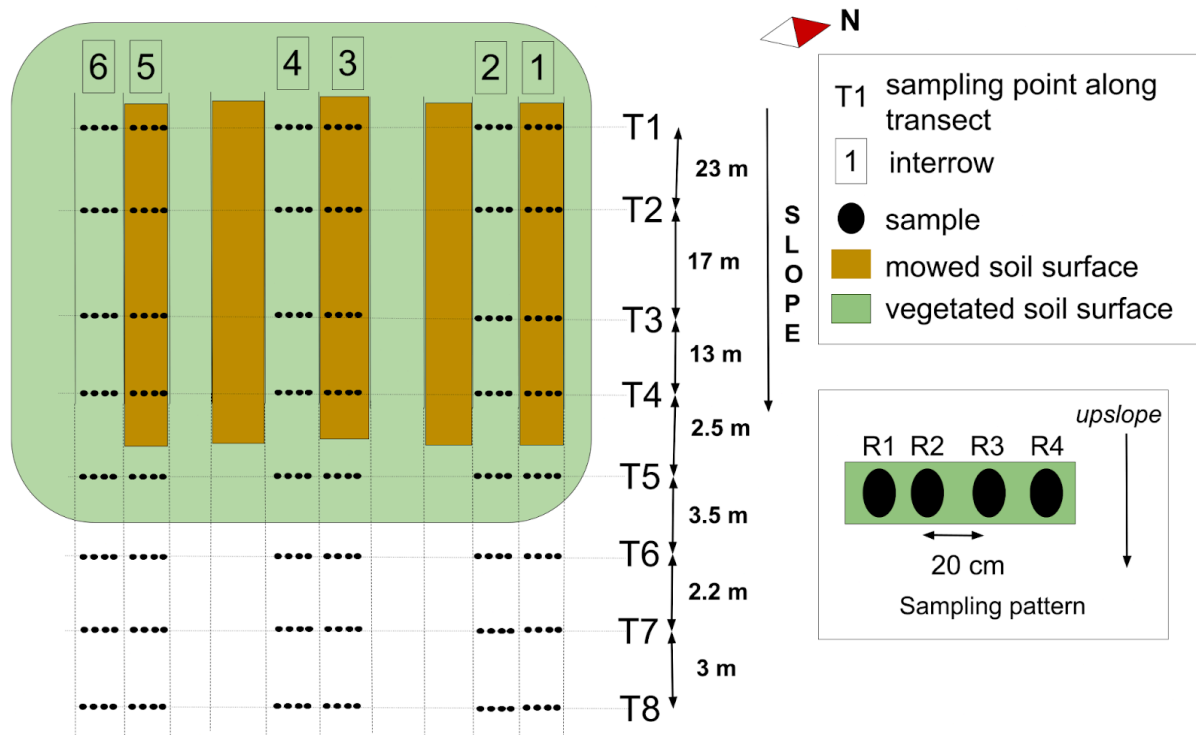


Figure II. 3. Representation of the Combaillaux vineyard (P2) sampling distribution and detailed sampling pattern. Each sample point represents 4 samples taken on a straight line approximately 20 cm from each other.

2.3. Seedling emergence method

Three days after the collection of the soil samples in the field (in April 2022), the 286 soil samples were placed in perforated plastic boxes (200x170x75 mm) on a layer of draining sand and covered with potting soil to facilitate germination. Before use, the potting soil was sterilized to ensure that it did not contain any organisms that could influence the development of the seeds (granivores, fungi, insects, etc.). The sterilization process included successive oven drying and then freezing the soil. The boxes were then placed randomly in an air-conditioned greenhouse (average $T^{\circ} = 22 \pm 3^{\circ}\text{C}$) on 3 separate benches. To ensure that the samples were not contaminated by exogenic seed input or seeds from other samples, one control box containing only sand and potting soil was placed on each bench. The samples were manually irrigated 5 days a week with tap water to maintain a constant moisture content throughout the experiment.

To trigger the emergence of the seeds of certain species from dormancy, a cold stratification period at 1°C was carried out for one month. The boxes were then placed back in the greenhouse in a randomized arrangement different from that prior to vernalization. The samples were also shuffled to stimulate germination (Price et al., 2010; Erfanzadeh et al., 2016).

Samples were monitored regularly to count and remove individuals sufficiently developed to be identifiable at the species level if possible and at the genus level otherwise using the Latin nomenclature as available in the WFO Plant List classification (<https://wfo.plantlist.org/plant-list/>). Poaceae were regularly replanted in individual pots to achieve a more precise identification without impacting the remaining seeds that may still germinate within the samples.

The spontaneous germination experiment took place over nine months. It was divided into two cycles: from April 2022 to July 2022 and from September 2022 to December 2022. The end of the experiment occurred after 2 weeks with the absence of seed emergence. Residual soil was not combed because the added information has been considered negligible in previous studies (Niknam et al., 2018).

2.4. Soil seed bank sampling representativity

To gain insight into how many species we might have missed, we used calculations developed for plant species composition surveys. This method is based on computing the theoretical species accumulation curve (SAC) by calculating the sum of generalized Simpson entropies based on subsampling using jackknife methods (Zhang and Zhou, 2010, summarized in Marcon, 2015). This method forecasts the effort needed to reach the “true” number of species in the sampled population. According to this method, we could have missed approximately 10 species in our sampled soil seed bank, which means that our results might have a bias of approximately 10%.

2.5. Dispersal modes

Species observed throughout the emergence period have been linked to their main dispersal mode using the TRY database (Kattge et al., 2020). Most species had several dispersal modes; thus, the most observed mode was selected. Among the 96 different species identified, 16 were primarily dispersed by anemochory, 11 by barochory, 15 by hydrochory and 54 by zoochory.

2.6. Statistical analyses

Eight different equations were used for generalized linear model (GLM) construction (Tab. 1), with separate GLMs constructed for each study site.

All data manipulation and statistical analyses were performed using R 4.2.2 (R Core Team, 2023) software. The Shannon index was computed for every sample using the entropart package (Marcon and Hérault, 2015) with a Chao, Wang & Jost correction (Chao, Wang and Jost, 2013) to take undetected species into account. The number of germinated seeds observed per box (=E) was related to the area sampled (=S, equal to 0.008 m²). Thus, the number of germinated seeds per surface unit obtained for each box, referred to as the "E/S ratio" (in number of plants per m²), was used for statistical analysis (Gaudichet et al., 2022). Vegetation cover was visually inspected at multiple points in every interrow sampled. In the Combaillaux vineyard, vegetation cover was on average between 90 and 100% inside the vegetated interrows and under 5% inside the unvegetated interrows. In the Roujan vineyard, vegetation cover was on average under 5% in all the studied interrows. Consequently, the analyses that included the effect of vegetation cover were only conducted on data collected within the field in the P2, and vegetation cover was included as presence/absence data in the models. Concerning the effect of dispersal mode on soil seed bank distribution, the number of germinated seeds observed for each main dispersal mode dispersal mode defined in the previous section was weighted by the number of species with this dispersal mode to avoid having an inflated E/S ratio caused by an overrepresentation of one particular dispersal mode.

The effect of the slope on the soil seed bank was tested using samples taken from the first 4 sampling points, which were used as a proxy for the slope gradient within the field. The sampled transect points were grouped into three zones: points T1 to T4 in the field (field zone), points T5 to T7 in the field edge (field edge zone), and points taken in T8 (ditch zone). The effect of landscape was not analyzed since the information would have been identical for every sample in each study site.

Because the number of germinated seeds was not normally distributed, our hypotheses were tested by constructing GLMs with a Poisson distribution, which eliminates the requirement for linearity and homoscedasticity of the data. Overdispersion of the residuals was detected; thus, a correction was applied using a quasi-GLM (Zuur et al., 2009). Based on a visual inspection, normality of the residuals and homogeneity of variances were met. Models were then tested using ANOVA tests.

To confirm that greenhouse position did not impact emergence, a GLM linking the E/S ratio to the sample location within the greenhouse was also constructed and tested with ANOVA. Greenhouse position did not have an impact on the number of seeds that germinated ($F = 0.44$, $p = 0.66$).

Table II. 1. Variables used for generalized linear model (GLM) construction. Separate GLMs were constructed for the two study sites, except for Equations 5 and 6, including the effect of the vegetation cover, which were only constructed using data from inside the field of the Combaillaux study site. Vegetation cover was included as presence/absence data in the models

Eq	Y	Explanatory variable(s)
1	E/S ratio	slope
2	Shannon index	slope
3	E/S ratio	zone
4	Shannon index	zone
5	E/S ratio	Interaction between zone and vegetation cover
6	Shannon index	Interaction between zone and vegetation cover
7	E/S ratio	Interaction between zone and dispersal mode

Differences between the coefficients computed for each GLM were tested by performing post hoc Tukey tests with the emmeans package (Lenth et al., 2023).

II. 3. Results

A total of 96 species were identified during our experiment, 52 of which were found in both study sites (Tab. II.2).

In the P2, the E/S ratio in T1 (upslope) was significantly higher (6160 +/- 6203 seedlings/m²) than the E/S ratio in T2 (steepest part of the slope) (2900 +/- 1969 seedlings/m²). However, we could not show such an effect of slope in P1 (Fig. 4).

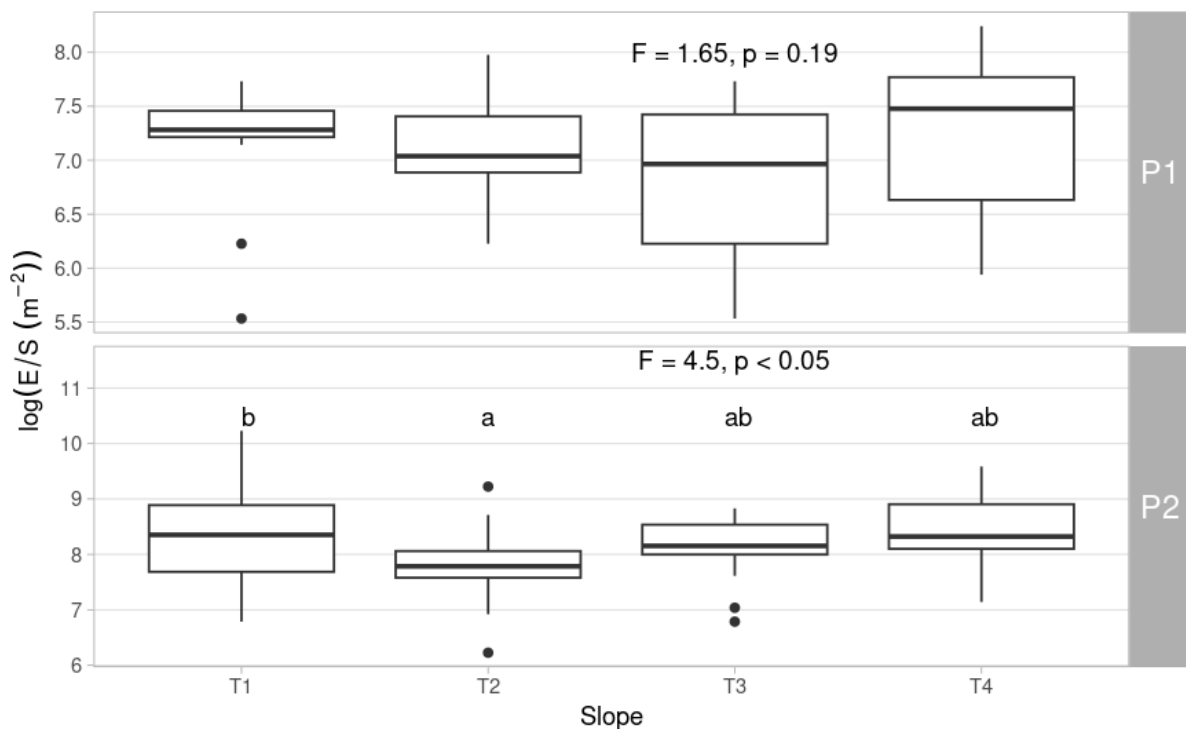


Figure II. 4. Distribution of the E/S ratio (in log scale) by sampling point within the field for P1 (Roujan vineyard) and P2 (Combaillaux vineyard). The slope effect was tested by ANOVAs on two separate GLMs constructed with data collected in P1 and the P2. T1 is situated before the start of the slope, T2 is at the start of the slope, T3 is at the end of the slope and T4 is at the bottom of the slope. In the plot displaying data from the P2, different letters indicate a significant difference between GLM coefficients.

Table II. 2. Number of species, first five most observed species and their respective contribution in samples found in each study site, in both study sites, and overall

	P1 <i>Roujan vineyard</i>	P2 <i>Combaillaux vineyard</i>	Shared	Total
Number of species observed	68	81	52	96
Most observed species	<i>Diptotaxis eruroides</i> (10.6%)	<i>Setaria pumila</i> (13.3%)	<i>Setaria pumila</i> (12.1%)	<i>Setaria pumila</i> (11.1%)
2nd most observed species	<i>Euphorbia prostrata</i> (9.3%)	<i>Portulaca oleracea</i> (12%)	<i>Euphorbia prostrata</i> (11.6%)	<i>Euphorbia prostrata</i> (10.7%)
3rd most observed species	<i>Poa annua</i> (9%)	<i>Chenopodium album</i> (11.5%)	<i>Portulaca oleracea</i> (10.3%)	<i>Portulaca oleracea</i> (9.5%)
4th most observed species	<i>Erigeron sumatrensis</i> (7%)	<i>Euphorbia prostrata</i> (11.2%)	<i>Chenopodium album</i> (10.1%)	<i>Chenopodium album</i> (9.3%)
5th most observed species	<i>Lysimachia foemina</i> (6%)	<i>Polygonum aviculare</i> (8.5%)	<i>Polygonum aviculare</i> (7.2%)	<i>Polygonum aviculare</i> (6.6%)

3.1. In-field effect of vegetation cover

The mean E/S ratio was significantly higher in samples originating from vegetated interrows (5329 +/- 4419 seedlings/m²) than in samples originating from tilled interrows (3773 +/- 3109 seedlings/m²; $t = 1.99$, $p < 0.05$).

The mean Shannon index was also significantly higher in samples originating from vegetated interrows (2.42 +/- 0.48) than in samples originating from tilled interrows (1.99 +/- 0.41; $t = -4.61$, $p < 0.01$).

We could not show a significant interaction of slope and vegetation cover on the E/S ratio ($F = 1.9$, $p = 0.12$). However, the interaction of slope and vegetation cover had a significant positive effect on the Shannon index (Fig. II. 5). The mean Shannon index from T3 (slope end) was significantly lower (1.95 +/- 0.43) in tilled interrows than in vegetated interrows (2.67 +/- 0.46; $p < 0.01$).

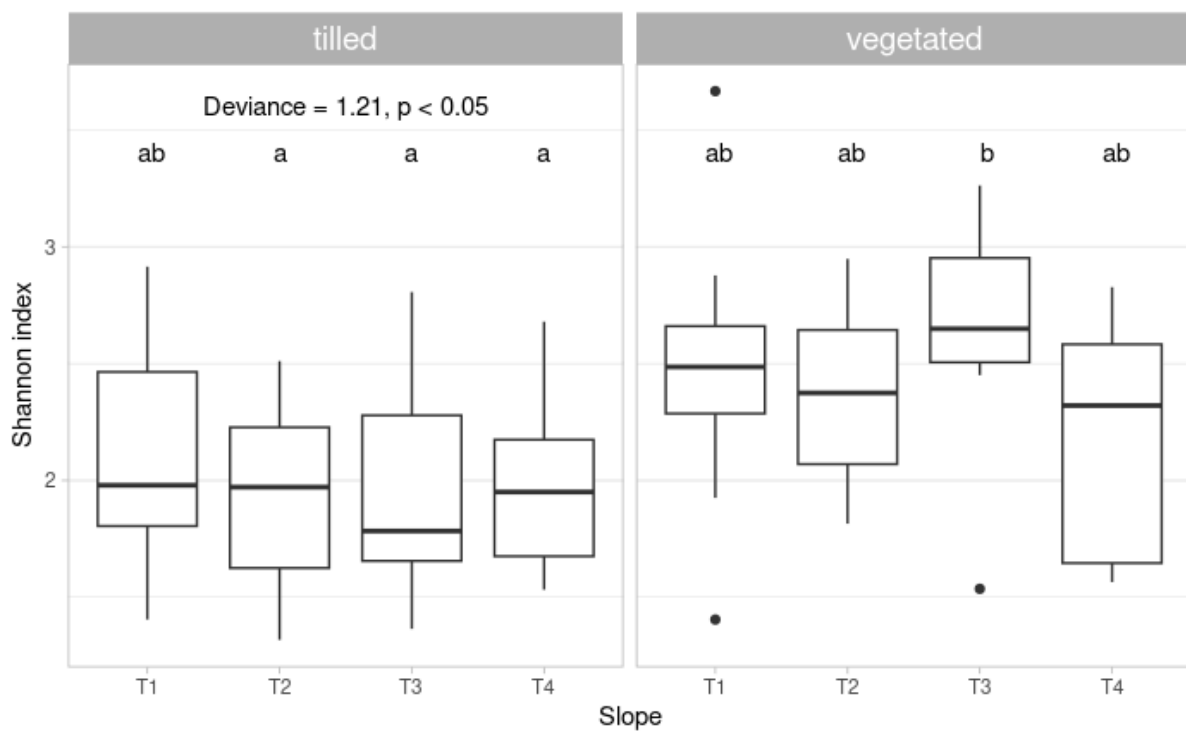


Figure II. 5. Shannon index computed for each sample grouped by slope point sampled for P2 (Combaillaux vineyard) only in tilled and vegetated interrows. The combination of the slope point and the presence of vegetation on the Shannon index was tested with ANOVA. T1 is situated before the start of the slope, T2 is at the start of the slope, T3 is at the end of the slope and T4 is at the bottom of the slope. The difference between all coefficients was tested with Tukey tests between all slope points, and different letters are used when differences are significant.

3.2. Zone effect

3.2.1. Effect of zone on the E/S ratio

Zone (i.e., the sample origin between the field, field edge and ditch) had a significant effect on the E/S ratio at both study sites. In the P1, the mean E/S ratio was lower within (1426 +/- 803 seedlings/m²) than outside the field (field edge: 3860 +/- 3953 seedlings/m²; ditch: 3144 +/- 1524 seedlings/m²). In the P2, the mean E/S ratio was lower at the field edge (3839 +/- 2760 seedlings/m²) than in the ditch (5759 +/- 2755 seedlings/m²; Fig. II. 6).

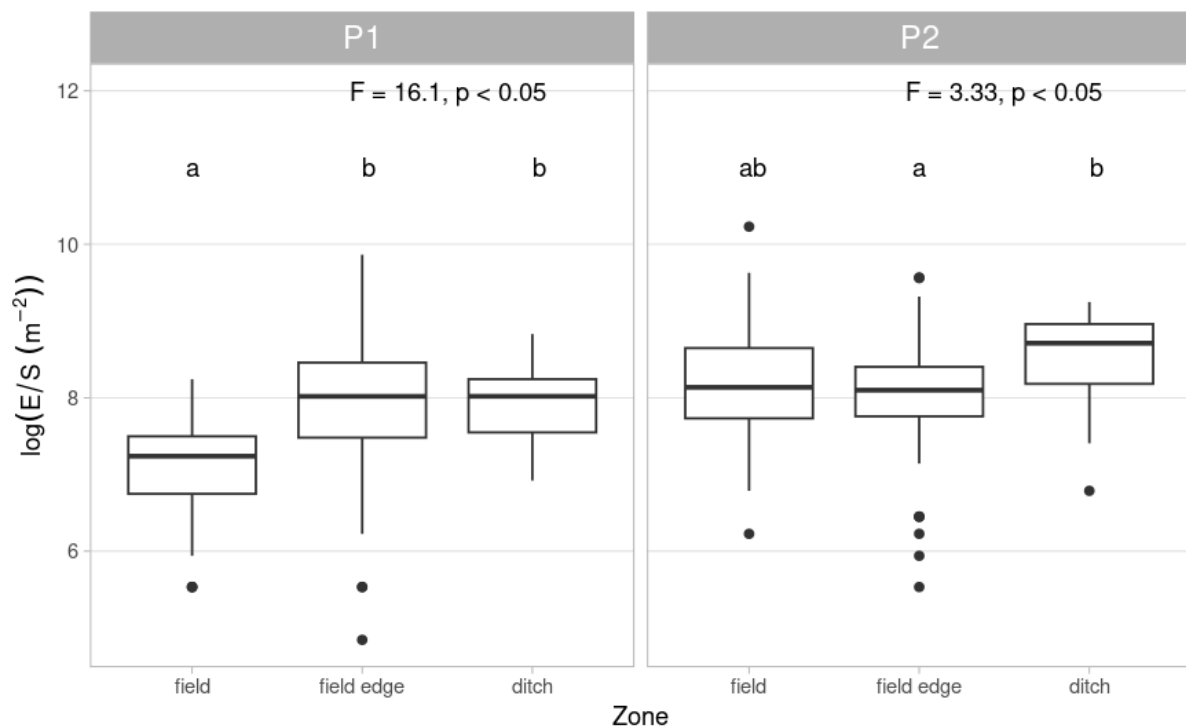


Figure II.6. Distribution of the E/S ratio (in log scale for readability purposes) in each sample, grouped by location in the study site, for P1 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. The “field” location represents samples taken within vineyard rows, the “field edge” location represents samples taken between the rows and the ditch, and the “ditch” location represents samples taken within agricultural ditches. The location effect was tested with ANOVAs, the difference between coefficients was tested with Tukey tests, and different letters are used when differences are significant.

3.2.2. Effect of zone on the Shannon index

Zone had a significant effect on the Shannon diversity index at both sites (Fig. 7). In the P1, the mean Shannon index was only significantly higher in the ditch (2.74 +/- 0.65) than in the field (2.13 +/- 0.64, $p < 0.05$), whereas in the P2, both the field edge (2.48 +/- 0.49, $p < 0.01$) and the ditch (3.49 +/- 0.49, $p < 0.01$) had a higher mean Shannon index than the field (2.20 +/- 0.49). The mean Shannon index was also significantly higher in the ditch than in the field edge (Fig. 7).

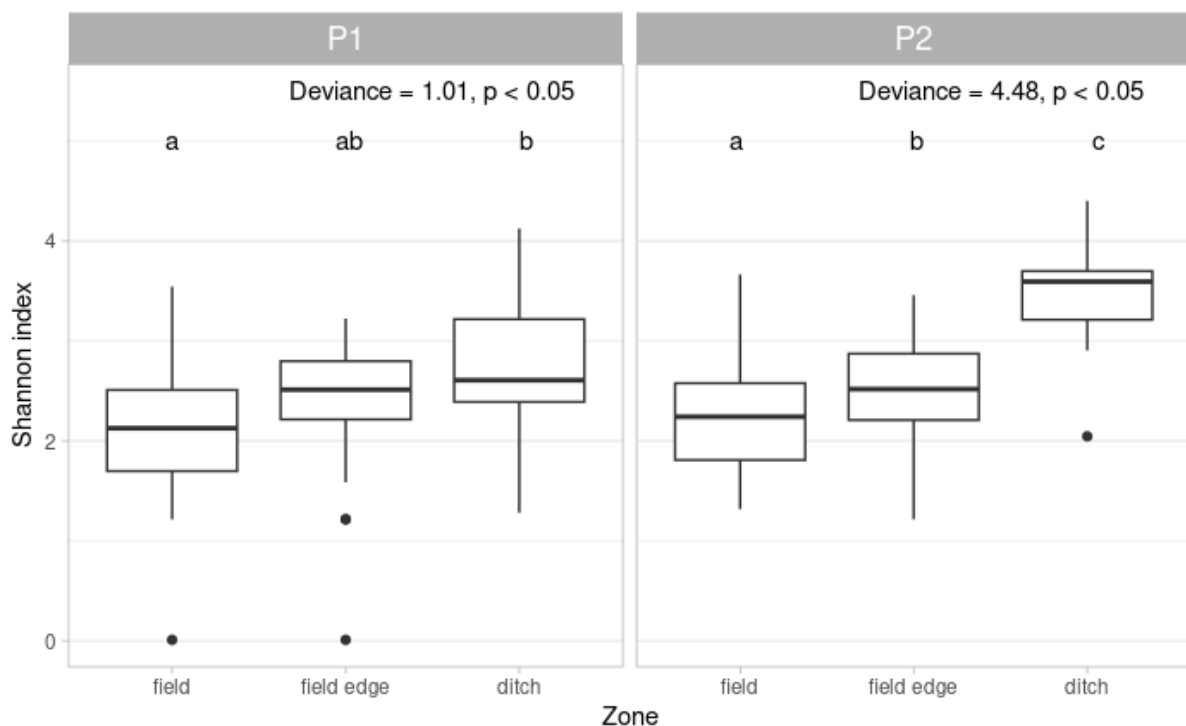


Figure II. 7. Shannon index computed for each sample grouped by location sampled for P1 (Roujan vineyard) and P2 (Combaillaux vineyard). The “field” location represents samples taken within vineyard rows, the “field edge” location represents samples taken between the rows and the agricultural ditch, and the “ditch” location represents samples taken within the agricultural ditches. The location effect was tested with ANOVAs. Differences between coefficients were tested with Tukey tests, and different letters are used when differences are significant.

3.3. Effect of dispersal mode on the soil seed bank

3.3.1. Effect of dispersal modes on the E/S ratio

The dispersal mode affected the overall E/S ratio observed at both study sites (Fig. II.8). At both sites, barochory was more prevalent than other dispersal modes (Fig. II.8). Additionally, in the P2, hydrochory was more prevalent than anemochory and zoochory (Fig. II.8; Appendix B).

The dispersal mode had a significant effect on the E/S ratio observed in each zone for both study sites (Fig. II.9; Appendix B).

In the P1, barochory was more prevalent than other dispersal modes at the field edge and in the ditch. In the P2, anemochory and zoochory were rarer than barochory and hydrochory in the field. Zoochory was also rarer than barochory at the field edge, and barochory was more frequent than hydrochory (Fig. II.9; Appendix B).

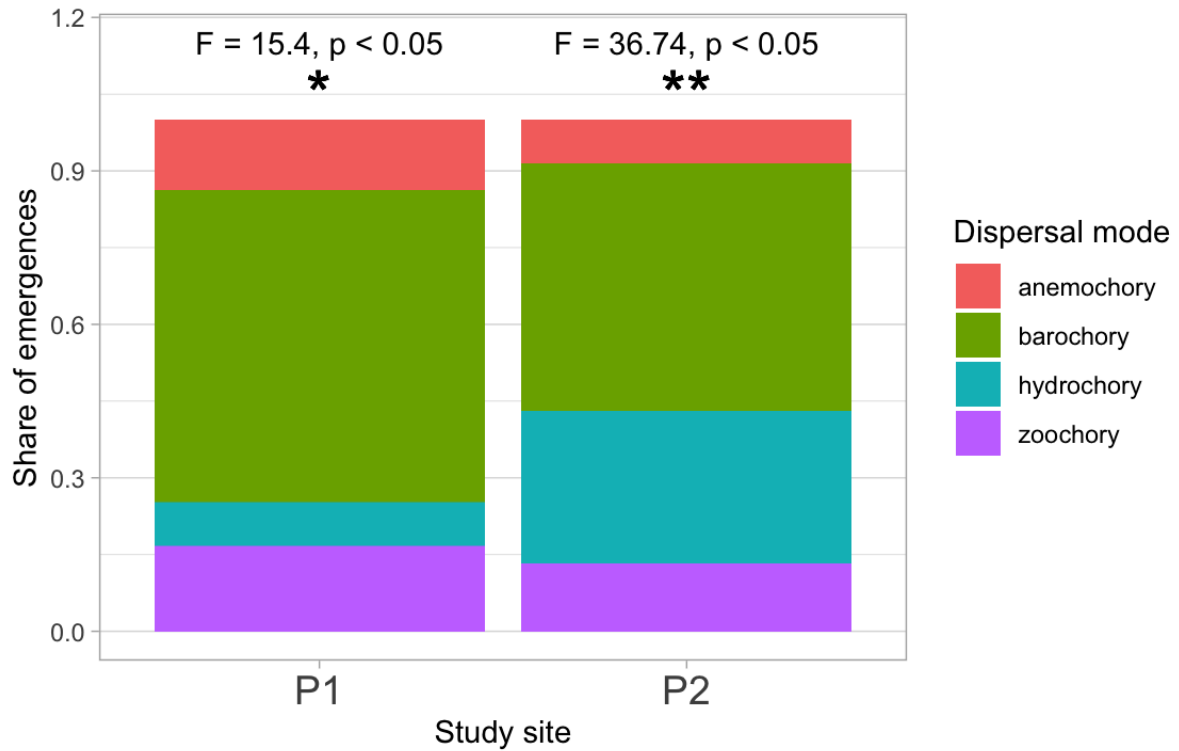


Figure II.8. Share of emergences for each dispersal mode for P1 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. Significant differences between dispersal modes using Tukey tests are represented using stars, one for each dispersal mode significantly different from the others.

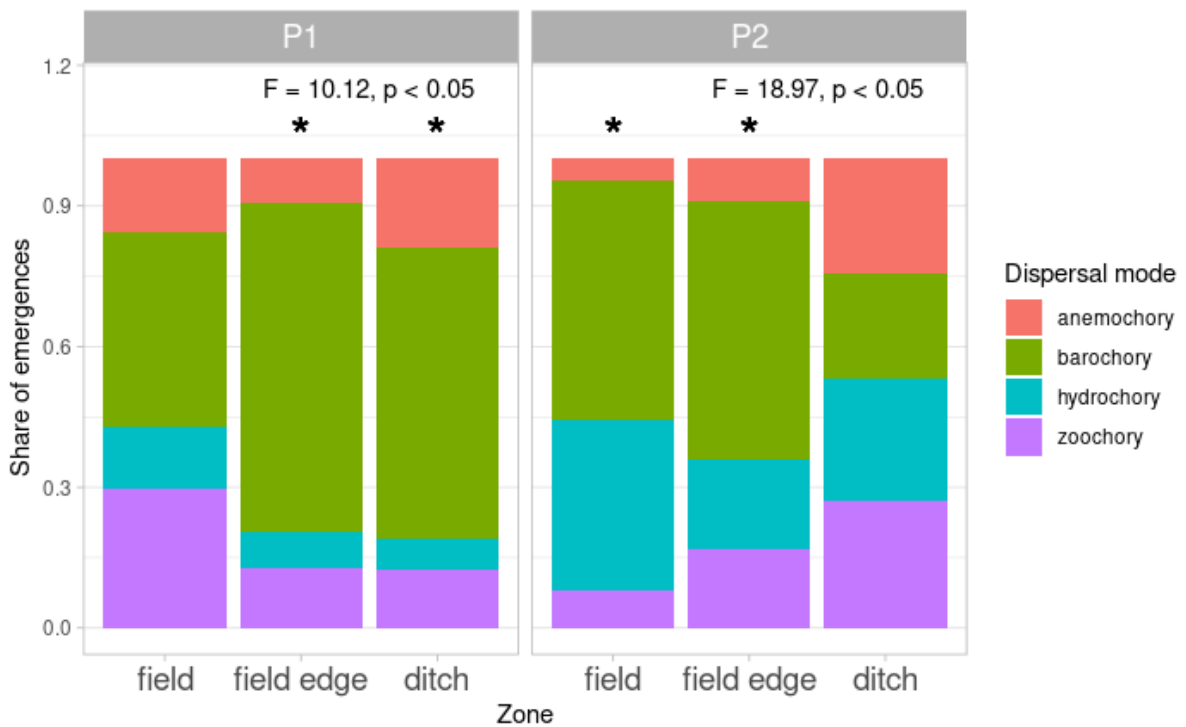


Figure II. 9. Mean E/S ratio by species for each dispersal mode, grouped by zone sampled, for P1 (Roujan vineyard) and P2 (Combaillaux vineyard). The “field” location represents samples taken within vineyard rows, the “field edge” location represents samples taken between the rows and the agricultural ditch, and the “ditch” location represents samples taken within the agricultural ditches. Significant differences between dispersal modes using Tukey tests are represented using stars, one for each dispersal mode significantly different from the others.

3.3.2. Influence of dispersal modes on the number of species

The dispersal mode had a significant effect on the number of species found in each zone at both study sites. More anemochorous species were observed outside the field than within both study sites. Additionally, the maximum number of anemochorous species was found within the ditch in both study sites. Last, more barochorous species were found in the field edge than in the field for both study sites (Fig. II.10; Appendix B).

In the P1, more barochorous species were found in the ditch than in the field. In the P2, the ditch hosted more hydrochorous species than the field and the field edge. Similarly, fewer zoochorous species were observed in the field than in the field edge and the ditch, and there were also fewer zoochorous species in the field edge than in the ditch (Fig. II. 10; Appendix B).

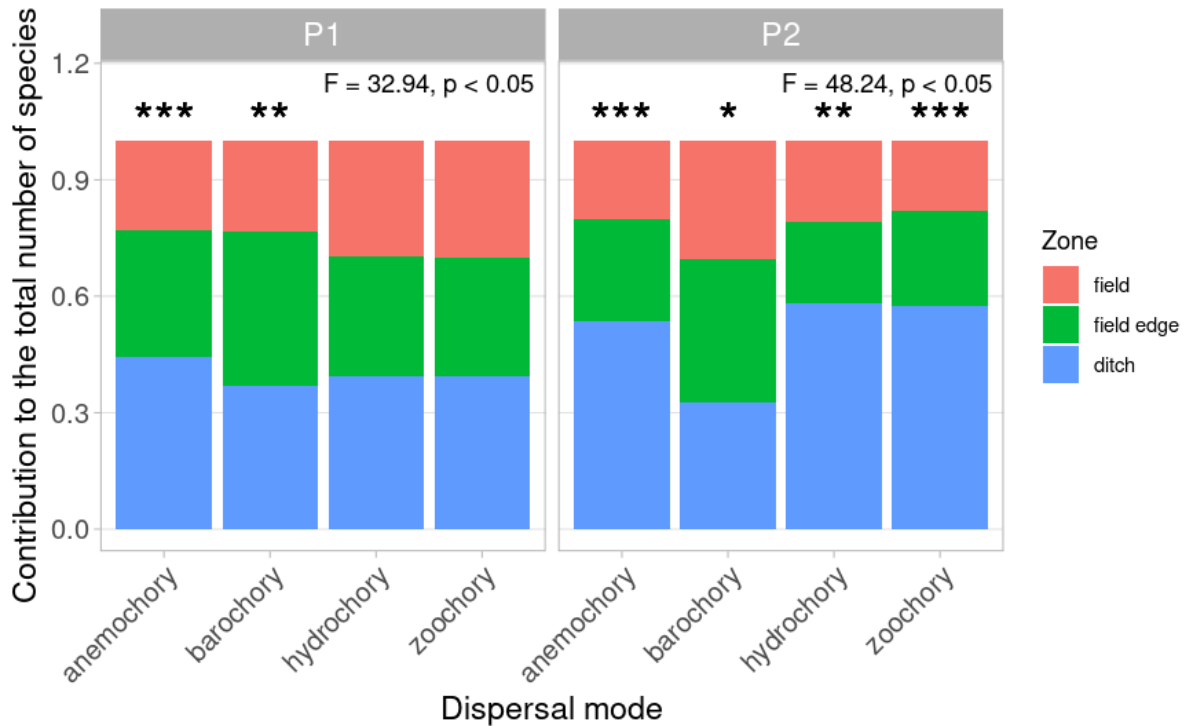


Figure II. 10. Contribution of each zone to the total number of species, grouped by dispersal syndrome, for P1 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. Significant differences between zones using Tukey tests are represented using stars, one for each zone significantly different from another.

II. 4. Discussion

4.1. Effect of vegetation cover in interrows on seed loss reduction

Our first hypothesis that the effect of the slope on soil seed bank density would be different between tilled and vegetated interrows was not supported. This result coincides with other works observing an absence of a link between seed loss and erosion (de Rouw et al., 2018). In their study, de Rouw et al. (2018) explained the possibility for seeds to be dispersed without the occurrence of soil erosion by the lower discharge necessary to move small and light seeds compared to the threshold value over which erosion starts, which might be the explanation for our results.

Nevertheless, the overall higher number of seeds that germinated in vegetated interrows and the higher species diversity gives credit to the expected benefits of vegetation cover on sloping conditions, which are more diverse than erosion control. While the benefits of

vegetation cover on the soil seed bank of woody crops have already been observed in different orchards (Carpio et al., 2020), the spatial configuration of a vineyard and the slope are differences important enough to consider these results noteworthy.

4.2. Soil seed bank diversity along the transect

The soil seed bank was found to be denser within the ditch than in the field in Roujan but not in Combaillaux. Our second hypothesis that the soil seed bank would be denser and more diverse inside the field margins and ditches than within the field was thus partially validated. Since chemical weeding inside the field is prevalent in Roujan and nonexistent in Combaillaux, it could be the factor that explains this difference between sites. Indeed, chemical weeding has been linked with soil seed bank depletion in previous studies (Andreasen et al., 2018).

The higher species diversity in the ditch found in both study sites is in accordance with the literature obtained on aboveground vegetation studies (Fried et al., 2012; Minarro, 2012; Holland et al., 2017; Cursach et al., 2020), which is interesting because the soil seed bank and the aboveground vegetation are not always similar in agrosystems (Andreasen et al., 2018). The results in the Combaillaux vineyard also indicate that interrows benefit from the field edge and the ditch as potential biodiversity sources, while the Roujan vineyard benefits only from the ditch. Thus, reducing chemical inputs benefits both the field and the field edges, which is in accordance with the expectations of land sharing (Fischer et al., 2014).

Like landscape in general, other factors, such as altitudinal gradient (Erfanzadeh et al., 2013), need to be accounted for when considering recolonization processes that stem from the soil seed bank of neighboring habitats.

Our results also need to be nuanced due to differences between our two study sites in both local conditions: annual precipitation and soil conditions, and the surrounding environment in terms of land uses and cumulative length of ditches. The higher length of ditches in Roujan than in Combaillaux could explain the higher diversity in the ditches, whereas the higher amount of seminatural habitats in Combaillaux could counterbalance the difference between sites. These doubts could be dispelled by implementing a new protocol based on more sites covering the region's soil and climate diversity to study the interparcel variability of the seed bank.

4.3. Dispersal mode and soil seed bank distribution

At both sites, dispersal mode played a role in soil seed bank distribution. Our results show that barochory is well represented within vineyards and their surrounding habitats, as was already reviewed by Benvenuti (2007) for agricultural environments in general. Barochory was prevalent outside the field both in terms of seed density and species in Roujan. However, the results were mixed in Combaillaux, where barochory was mostly observed within the field in terms of seed density but outside the field in terms of the number of species. Because the mean slope is 15% in Roujan and 20% in Combaillaux, the beneficial effect of slope on dispersal by barochory is not straightforward in our results. In Combaillaux, it is possible that practices favored a few opportunistic species within the field, whereas conditions outside the field allowed more species with different dispersal modes to develop.

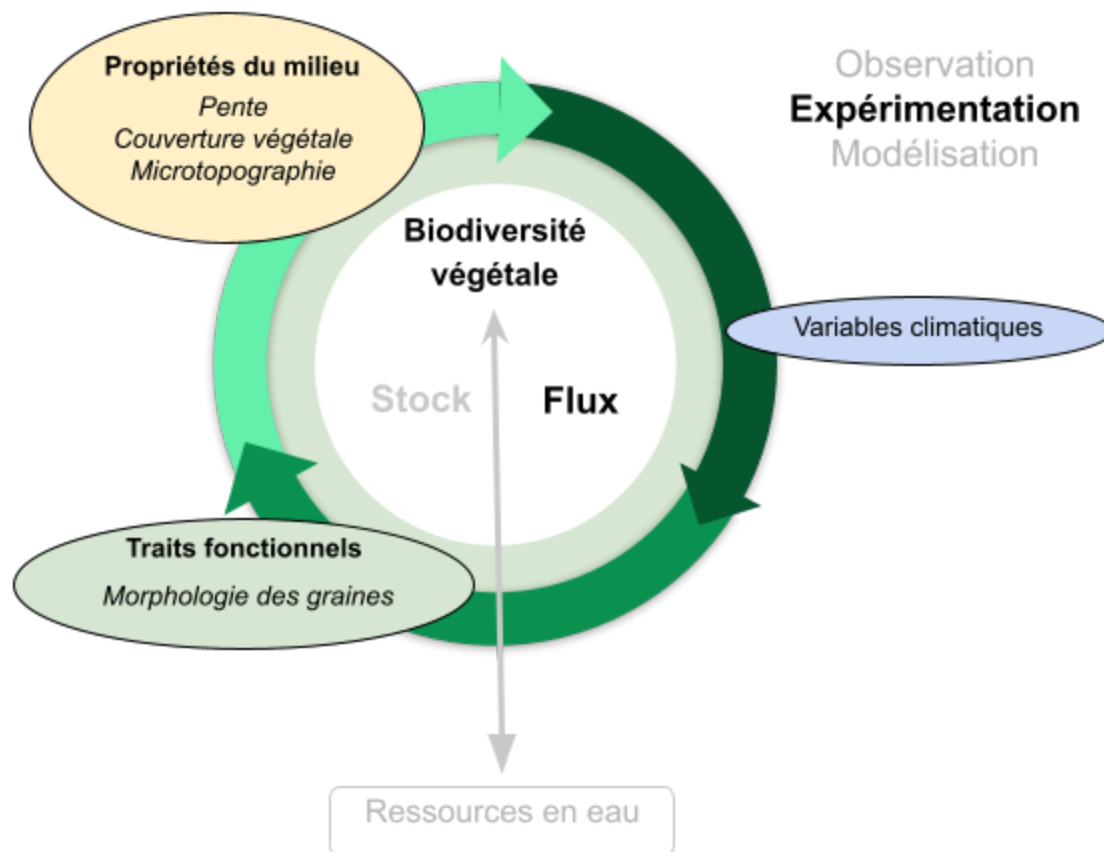
Concerning the distribution of hydrochorous species, we only observed more species in the ditch for the Combaillaux site and found no differences in terms of the number of seed counts. The absence of a higher number of hydrochorous species within the ditch in Roujan is likely due to the site position on the upper side of the Roujan catchment, which makes it a likelier site for seed detachment than retention due to its hydrological regime and its slope (Calçada et al., 2015; Fraaje et al., 2017; West et al., 2020; Su et al., 2022). An additional explanation could be the length of the ditch network, which is almost 3 times longer in Roujan than in Combaillaux; thus, seeds have more space to disperse.

As agricultural ditches can act as biodiversity corridors and refuges (Herzon and Helenius, 2008; Dollinger et al., 2015), it is not surprising to observe more zoochorous species within the ditch than within the field, although this result was observed only in Combaillaux. In Combaillaux, presence of carabids, small mammals and ants was observed, whereas in Roujan only ants were observed. This difference could be explained by the landscape, especially by the share of seminatural habitats, which is higher in Combaillaux (55%) than in Roujan (10%), because seminatural habitats are important biodiversity refuges (Garibaldi et al., 2021; Tschardt et al., 2021).

4. 4. Conclusion

To our knowledge, this study was one of the first to study the effect of management practices on the soil seed bank from inside a field to the bottom of an agricultural ditch. Another noteworthy result of this study is the observation that vegetation inside the interrows did not significantly reduce the depleting effect of the slope on the soil seed bank distribution, despite the well-known role of erosion reduction on vegetation and seed loss. These preliminary results, should they be confirmed by further studies, could influence weeding practices in vineyards in order to maximize potential benefits from a rich soil seed bank inside agroecosystems. To confirm the related hypothesis we made to explain some of our results, further work investigating the influence of landscape on the soil seed bank is needed.

Chapitre III. Expérimentation sur l'hydrochorie par ruissellement de surface



Après avoir étudié les facteurs d'influence de la banque de graines du sol dans le chapitre précédent, avec notamment la prise en compte du mode de dispersion, ce chapitre porte sur l'étude de l'hydrochorie lors d'un épisode de ruissellement au sein d'une parcelle viticole méditerranéenne. Plus spécifiquement, l'article constituant ce chapitre s'est intéressé à l'influence de la pente, du couvert végétal ainsi que la rugosité d'une section de sol sur la proportion de graines l'ayant traversé.

L'article qui suit a été soumis à la revue *Ecohydrology* en 2024 sous le titre *Secondary seed dispersal by hydrochory during surface runoff inside a Mediterranean vineyard*.

III. 1. Introduction

The diversification of crop and non-crop habitats in agroecosystems is a major challenge for modern agriculture (Hatt et al., 2018). This is particularly true in the Mediterranean region, which is considered a hotspot of climate change (Cozannet et al., 2021) and a laboratory for agroecological transition to make vineyards more resilient to climate change (Hannah et al., 2013).

In Mediterranean vineyards, management practices based on spontaneous vegetation cover or the sowing of service plants between rows are promoted as part of the agroecological transition (Fernandez-Mena et al., 2021). In these vineyards, vegetation cover is sometimes maintained in one of two or four interrows to reduce the amount of soil lost to erosion (Novara et al., 2011). The other interrows are generally plowed to avoid competition for water between the vegetation cover and the vines (Garcia et al., 2018; Celette et al., 2010).

Water resources are the main factor determining the functioning of Mediterranean agroecosystems (Hannah et al., 2013). Both lack of water resources (Celette et al., 2010) and excessive rainfall (Borelli et al., 2017) can be limiting factors for plant growth. Water flowing in Mediterranean landscapes passes through a variety of elements, carrying both biotic (i.e., plant propagules) and abiotic (i.e., soil particles) matter, providing benefits (i.e., seed dispersal) but also drawbacks (i.e., soil erosion).

The circulation of soil particles by water is well documented in studies of soil erosion processes. Seed dispersal by water (i.e. hydrochory), on the other hand, has primarily been studied in permanent streams (Soomers et al., 2010; 2013; Thompson et al., 2014; Carthey et al., 2016). However, hydrochory can also occur during surface runoff (Fryirs and Carthey, 2022; Su et al., 2022) and can play an important role in the secondary dispersal process of plants when surface runoff carries seeds into permanent water streams (Thompson et al., 2014; Vander Wall and Longland, 2004). Secondary dispersal describes the potential for seeds to be dispersed by two separate dispersal events, thereby increasing the total dispersal distance (Wehner et al., 2020). Seed dispersal is essential for supporting plant biodiversity and is therefore a key part of agroecological transition (Potschin-Young et al., 2018; Thompson and Katul, 2009).

Seed dispersal has been observed in studies of soil loss by erosion (Han et al., 2011; de Rouw et al., 2018; Janeau et al., 2022). Experiments have demonstrated a facilitating effect of slope (Han et al., 2011; Jiao et al., 2011) and a negative effect of surface roughness on seed

dispersal distance during runoff (Aerts et al., 2006; Isselin-Nondedeu et al., 2006). However, most studies have been conducted using artificial rainfall, which may have different results than natural rainfall (Yu et al., 2017). Furthermore, although studies in soil science have found that the association between soil surface properties and seed dispersal patterns depends on seed morphology (Bochet, 2015), it is rarely considered in ecological studies (Tekiel and Barney, 2013; Aerts et al., 2006).

Round seeds are assumed to be easily dispersed by water flow, and are more likely to be moved by runoff than other seed morphologies (Bochet et al., 2015). In contrast, plumed seeds are mainly dispersed by wind (Benvenuti, 2007) and are less likely to be removed by runoff along with other seeds with appendages such as hooks (Garcia-Fayos et al., 2010). Nevertheless, secondary dispersal events often occur thanks to dispersal modes that differ from the main mode of each species (der Werduwen & Ruxton, 2019). Characterizing the extent to which seeds primarily dispersed by wind or animals are dispersed by surface runoff, will provide new insights on potential dispersal capacities of plant species.

Inside vineyards, alternance between vegetated and plowed interrows creates differences in soil surface properties. In a study tracking seeds dispersed by hydrochory in drainage ditches, Soomers et al. (2010) developed a conceptual model for hydrochory by dividing ditches into 2 m sections and characterizing vegetation, surface aspect, and slope for each of these sections. Based on this information, the permeability of each section to seeds was estimated as the proportion of seeds observed beyond the section to the total number of seeds observed. Adapting this experimental design to study hydrochory during surface runoff would provide a basis to compare the interaction between surface properties and their permeability to seeds.

In surface runoff, hydrochorous seeds must first be detached from the soil before they can begin to disperse. In this context, the analysis of hydrochory must include an analysis of the factors that influence the detachment of seeds from the soil before examining the factors that influence the dispersal pattern. Factors influencing the detachment of seeds from soil can be defined as extrinsic factors, such as surface runoff features, slope, vegetation cover, and surface roughness (Garcia-Fayos et al., 2013), and intrinsic factors, such as seed density and seed morphology (Wang et al., 2013).

In this study, we aimed at investigating secondary seed dispersal by hydrochory mediated by surface runoff. We formulated three main hypotheses : (H1) the proportion of dispersed seeds over the total number of seeds placed on the ground for the experiment is explained by specific soil surface properties, seed morphology and surface runoff features, (H2a)

vegetation cover and soil roughness reduce soil permeability to seed dispersal, whereas high values of slope degrees favor seed dispersal, and (H2b) the dispersal pattern of round seeds is less affected by soil surface properties than other seed morphologies.

III. 2. Material and Methods

III. 2.1. Study site

We selected an experimental plot located in a vineyard of Merlot grape variety situated north of Montpellier (south of France, 43.659903, 3.767451). The climate is classified as Mediterranean and subhumid, with an average rainfall of approximately 600 mm per year over the 2011-2020 period (Météo France). Rainfall events are usually of high intensity and short duration, with a high interannual variability.

The vineyard is HVE-certified (Haute Valeur Environnementale - High Environmental Value), which indicates a low use of synthetic chemical inputs, an important number of vegetated interrows, and a required proportion of diversified non cultivated zones (i.e. hedgerows, ditches, fallow, etc.) inside the total surface of the vineyard.

The plot area was approximately 3 ha. It was characterized by a calcosol and a mean slope of 20%. Rows were oriented from east to west. An agricultural ditch downstream of the plot collected run-off water. In September, every second row is mowed and plowed after the harvest and then sown, and the remaining rows are simply plowed.

III. 2.2. Experimental setup

Six interrows were used, in 3 groups of 2 adjacent interrows, one plowed and the other vegetated. Studied groups of interrows were spaced 5 m apart (2 interrows) (Fig. III.1).

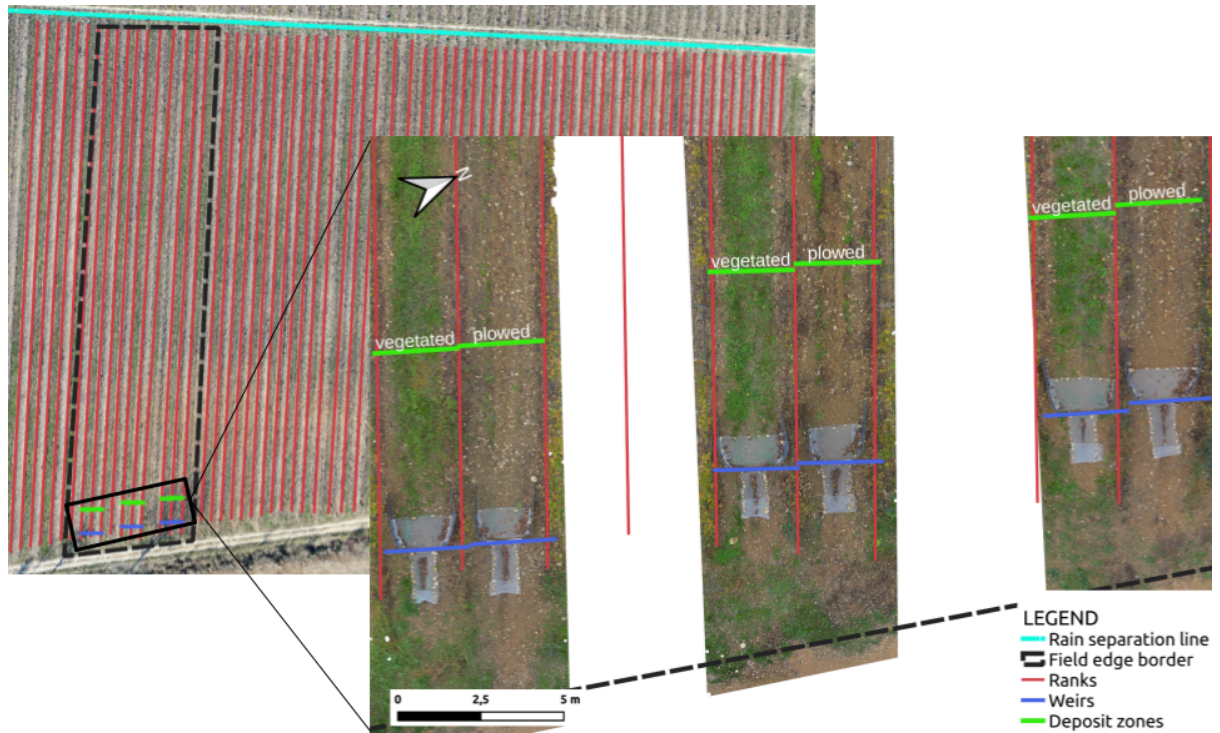


Figure III. 1. Aerial view of the plot used for the experiment, delimitation of the zone used, and focus on the experimental setup. The experimental setup consisted in six weirs placed at the end of the interrows (blue lines), associated with fine-mesh nets placed before and after the weirs to trap seeds. The seeds used for the experiment were placed 6m inside the interrows (green lines).

To characterize runoff events, flat V-weirs with plastic structures designed to redirect incoming runoff from an entire interrow were installed at the bottom of each interrow (Fig. III. 2). Fine-mesh nets (with mesh size smaller than the diameter of the seeds used in the experiment) were placed before and after the weirs to trap seeds.

Sensors (Onset HOBO Water Level Data Logger 0-4m, typical error : +/- 0.4 cm) were placed next to each weir and set up to record the water level every 10 seconds. Water level (h, in m) was converted into flow rates (Q, in m³.s⁻¹) using the formula for V-weirs used in the Cassiopée software (Eq. (1), Dorchies et al., 2022) :

$$Q = Cd \times \tan\left(\frac{\theta}{2}\right) \times h^{2.5} \quad (1)$$

The discharge coefficient (Cd) was set as 1.37 (the value associated with this formula), θ was 60°, and h the value measured by the water sensors.

The maximum discharge recorded in each interrow (converted in l.s⁻¹) was used to test the effect of runoff intensity on seed detachment, as expected in our first hypothesis.

An automatic rain-gauge was also installed on the plot to measure the total rainfall and the rainfall intensity locally.



Figure III. 2. Experimental setup installed at the end of the six interrows used for the experimentation. The setup is composed of a calibrated wooden weir equipped with PVC panels redirecting runoff towards the weir, and nets laid on the ground to facilitate sediment recovery for further analyses. Water level sensors were placed parallel to the weirs on the side facing the slope.

For each interrow, two digital elevation models (DEM) and orthoimages at 1 mm resolution were constructed using the Structure-from-Motion (SfM) approach with a multi-view Stereo algorithm for soil surface properties computation (Vinatier et al., 2018). Before and after the experiment, images were collected using a Canon 3200 camera attached to a 3m stick, and walking alongside the interrows used for the experimentation. Both campaigns were processed together in the SfM toolchain in order to align the resulting DEMs, following the TimeSIFT approach (Feurer and Vinatier, 2018).

III. 2.3. Seed selection and marking

Three species were selected in order to represent contrasting morphologies of seeds produced by species found in Mediterranean vineyards : small round seeds (poppy, *Papaver rhoeas*), plumed seeds (cane bluestem, *Bothriochloa barbinodis*), and hooked seeds (wild carrot, *Daucus carota*). *P. rhoeas* seeds were bought, while *B. barbinodis* and *D. carota* seeds were manually collected on wild patches of vegetation prior to the start of the experiment. The longest length (in mm) and the shortest length of the seed (in mm) were measured with calipers on 10 seeds from each species and then averaged. The mean dry mass (in mg) of the seed was measured by weighting 10 samples of 100 seeds of each species, using a high-precision balance (Precisa XB 160M, precision : 0.001 g and accuracy : 0.01 g). For

each species, the mass over volume ratio (in mg.mm-3) was calculated. To calculate the volume of *D. carota* and *P. rhoeas* seeds, their morphology was assimilated to a sphere and the corresponding formula was used, whereas *B. barbinodis* seeds were assimilated to cylinders.

Fluorescing powders (distributed by LDP-LLC, Carlstadt, USA) were used for marking seeds, as proposed by Tekiela & Barney (2013). Fluorescing powders were preferred to spray paint (Zhang et al., 2022; Chaudron and Isselin-Nondedeu, 2017), which allows for on-site seed marking, but could change the way seeds are perceived by granivorous animals (Kempster et al., 2018).

We estimated buoyancy duration following the protocol described by Boedeltje et al. (2003). A total of ten samples of 50 seeds of each species were placed in polyethylene cylindrical bottles filled with tap water. Immediately after the start of the experiment, the bottles were shaken for 5 s and the number of floating seeds was counted. Then, bottles were shaken every 30 minutes for the first four following hours (i.e., 8 repetitions), and daily during the following two weeks. The time periods after which 50% (t_{50}), 90% (t_{90}), and all of the seeds (t_{max}) had sunk were determined (Table III.1).

Table III. 1. Characteristics of the seeds used for the experiment. t_{50} , t_{90} , and t_{max} are the time periods after which 50%, 90%, and all of the seeds had sunk, respectively. The term used to refer to the seed morphology of each species is specified in parentheses next to their names.

	Species (morphology)		
	<i>B. barbinodis</i> (plumed)	<i>D. carota</i> (hooked)	<i>P. rhoeas</i> (round)
Mass (mg, mean +/- SD)	18.72 +/- 0.55	1.53 +/- 0.09	0.40 +/- 0.02
Length (mm, mean +/- SD)	5.24 +/- 0.65	4.0 +/- 0.56	1.78 +/- 0.29
Width (mm, mean +/- SD)	1.79 +/- 0.37	2.59 +/- 0.6	1.17 +/- 0.22
Mass/volume ratio (mg.mm-3)	0.70	0.04	0.13
Instant buoyancy (%)	100	94	88
t_{50} buoyancy (min)	270	1080	24.
t_{90} buoyancy (hours)	24	108	14
t_{max} buoyancy (days)	9	12	4

For each species, six samples of approximately 10000 (+/- 250) seeds were marked (i.e. one sample for each interrow, approximately 60000 seeds marked for each species). Samples were prepared by weighing 187.2 g, 15.3 g, and 4.0 g of *B. barbinodis*, *D. carota*, and *P. rhoeas* seeds respectively. Samples were then marked using the fluorescing powders (UVXPBR or UVXPBY powders), and different colors were used to differentiate between plowed and vegetated interrows. The use of those specific fluorescing powders had not been shown to affect the floating behavior of seeds (Rudi et al., 2018), and preliminary experiments confirmed this observation ($F = 0.16$, $p = 0.85$, Appendix C1).

III. 2.4. Seed release event

Based on meteorological records during previous decades, high intensity rainfall events were searched for between 15/10/2022 and 15/03/2023. This time of year also corresponds to a decrease in the frequency of practices in the field, which reduced the probability of changes in soil surfaces unrelated to runoff.

On the 15/12/2022 at 10h30, 30 000 marked seeds (10 000 for each species, 10 times more than the amount used by Soomers et al., 2010) were spread in a 2.5*0.30m band, 6 meters upstream from the end of the interrows. This surface will be referred to as the seed deposit zone in data analyses. Seeds were placed on the ground when runoff was visually observed, in order to study secondary dispersal. Seed dispersal was assessed the same day at nightfall to detect fluorescence of seeds by using UV lights. At each location where a group of seeds was observed between the seed deposit zone and the weirs, a numbered plastic marker was placed on the ground and the visual seed count (noted DS) was written down alongside the marker index. The exact position of the markers was determined using differential GPS data. Seeds still observed in the seed deposit zone will be referred to as unmoved seeds (US).

III. 2.5. Characterization of soil surface properties, seed count, and section permeability to seeds

Three soil surface properties were calculated considering their potential impacts on seed dispersal and on soil particles transport: the slope (SL), the fractional vegetation cover

(FVC), and the surface roughness (SR, Fig. 3). Other soil surface properties (bulk density, texture, structural stability) were not considered in the analyses because their values were similar over the total surface considered.

In each interrow, the 6m between the deposit zone and the weir were decomposed in 2.5*0.30m sections (i.e. 20 sections per interrow) to have local values for soil surface properties (Sommers et al., 2010). Soil surface properties were averaged at the scale of each section

Orthoimages and resulting DEMs with an initial 1 mm resolution were aggregated to a 1 cm resolution to reduce error in the calculation of soil surface properties.

For FVC calculation, a raster derived from the orthoimages was created by associating a unique value to each combination of red, green, and blue values of the raster bands composing the orthoimages. The values associated with green vegetation were then identified and used to create a second raster where each raster value was associated with vegetation (1) or not (0). The FVC (in %) was then estimated as the averaged pixel values inside each section multiplied by 100. Resulting FVC values were then classified into low (<25%), medium (25% - 50%), and high (>50%) classes (Fig. 3).

SL (in %) was calculated for each section as the elevation difference between the mean elevation of the upper and lower sides of the section, divided by the distance between the two sides (0.3 m), and multiplied by 100. Resulting SL values were then classified into low (10 - 25%), medium (15 - 17.5%), and high (>17.5%) (Fig. 3).

SR was calculated by computing the difference between the maximum and the minimum elevation (in m) inside a 3x3 radius for each 1 cm² pixel (Wilson et al., 2007). Then the mean SR value over each section was calculated, and multiplied by 1000 to obtain values in millimeters. Resulting SR values were then classed as low (0 - 10 mm) medium (10 - 20 mm) and high (>20 mm) (Fig. 3).

Counts of DS associated with each marker were aggregated by section.

The permeability of a section j to seeds (PS) was determined for each seed morphology i . PS was calculated as the number of seeds dispersed farther than the section (DS_{FAR}) over the total number of dispersed seeds (DS_{TOT}).

$$PS_j^i = \frac{DS_{FAR}^i}{DS_{TOT}^i}$$

Sections were drawn as polygons on QGIS software, and data treatments were performed using R software (R CORE Team, 2017) and the terra package (Hijmans et al. 2024).

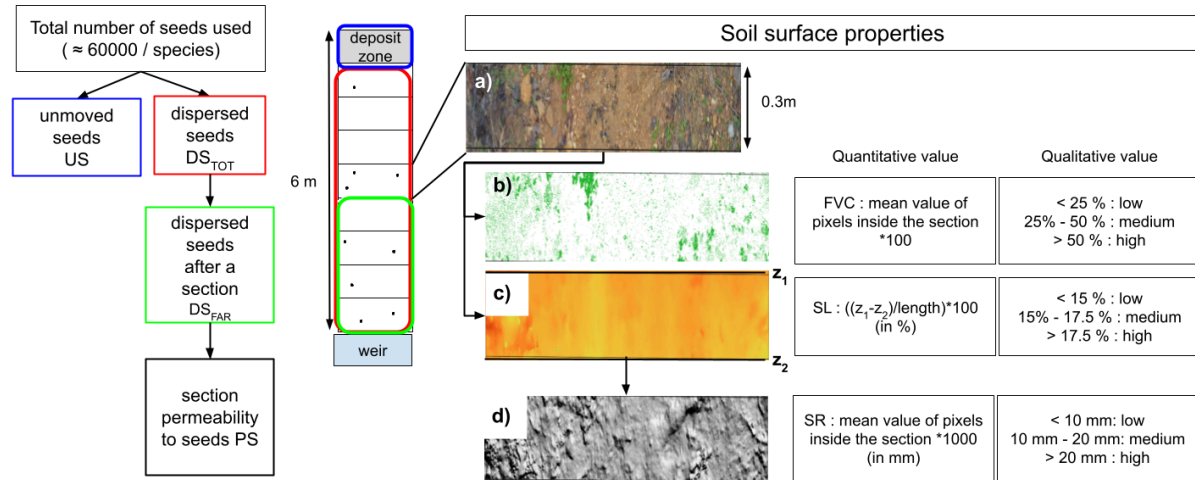


Figure III.3. Conceptual representation of the experimental setup and associated variables. Computation of soil surface properties is detailed, with (a) the original orthoimage, (b) the vegetation raster derived from it, (c) the DEM, and (d) the hillshade map.

III. 2.6. Statistical analyses

Our first hypothesis (H1) on the relation between (i) the proportion of dispersed seeds and (ii) soil surface properties, seed traits, and discharge, was tested on unmoved seeds (US). We performed a multiple regression analysis, with US as dependent variable, and FVC, SL, SR, the mass volume ratio, and the maximum discharge measured as explanatory variables. Our second hypothesis on the relations between soil surface properties and seed dispersal patterns without discriminating between seed morphologies (H2a) and for each seed morphology (H2b) were tested on each section permeability to seeds (PS). Because PS was not normally distributed and heteroscedasticity of the grouping variables was detected, nonparametric pairwise comparisons tests were used (Wilcoxon and Kruskal-Wallis) for H2. Bonferroni corrections were then used to adjust p-values to multiple comparisons.

All statistical analyses were performed using R software version 4.3.2 (R CORE Team, 2017).

III. 3. Results

3.1. Dispersal event

On 15/12/2022, the total rainfall was over 60mm, the highest rainfall event of December 2022. Between the time of seed release and the time of seed counting, 15mm of rain was measured, with a maximum intensity of 35 mm.h⁻¹, 30 min after the start of the experiment (Fig. III. 4). Significant runoff was detected only in plowed interrows, with a mean maximum value of 1.39 +/- 0.34 l.s⁻¹ (Tab. III. 2). In vegetated interrows, runoff was 0.08 +/- 0.05 l.s⁻¹ (Tab. III. 2).

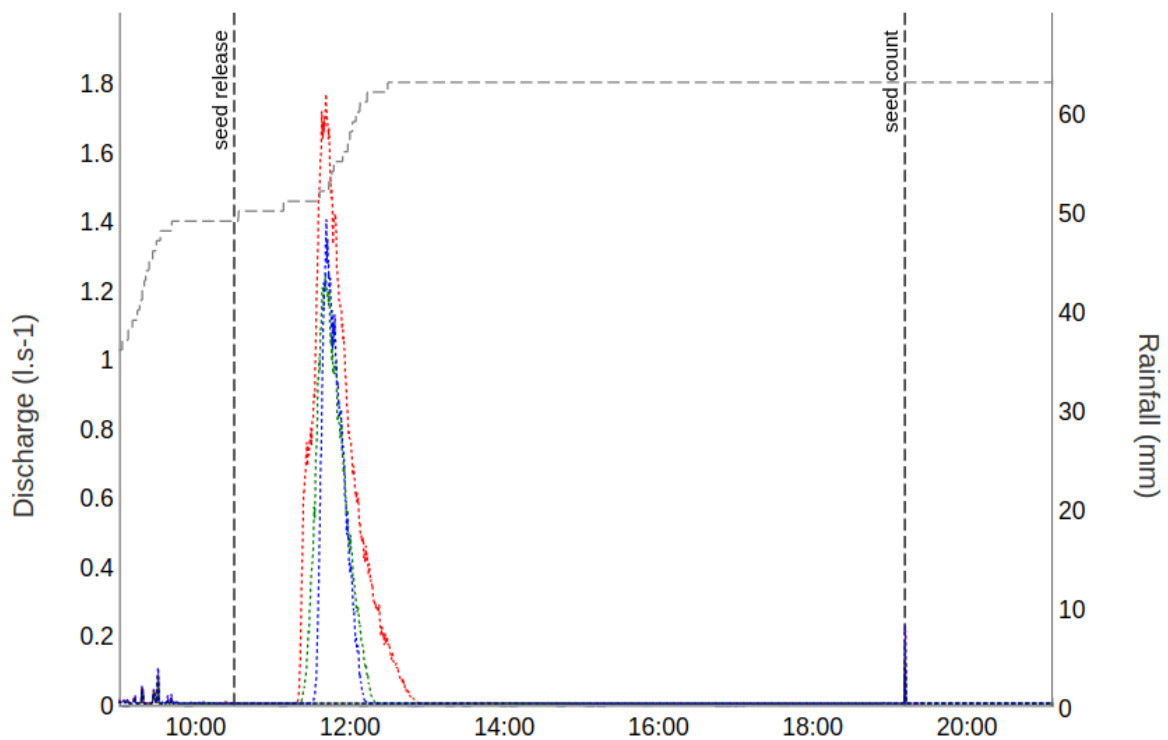


Figure III.4. Measured discharge (colored lines) and rainfall (gray line) during the experiment. The red, green, and blue lines correspond to the three plowed interrows respectively, out of the 6 interrows sampled. Dotted vertical lines correspond to the time of the seed release and the start of the seed count, respectively. The vertical lines also mark the moment the water level sensors were placed and then removed.

SL ranged from 10 to 25% across all sections, FVC ranged from 0 to 20% for plowed interrows, and from 15 to 60% for vegetated interrows. Lastly, SR ranged from 0 to 40mm (Fig. III. 5).

Table III.2. Overview of the main results obtained from the experiment, summarized by the state of the vegetation

	Plowed interrows	Vegetated interrows
Seeds at the weir (%)	10	0
Maximum discharge ($l.s^{-1}$)	1.39 +/- 0.34	0.08 +/- 0.05
Mean seed dispersal distance (m)	4.65	0.25
Total seeds observed	1746	87

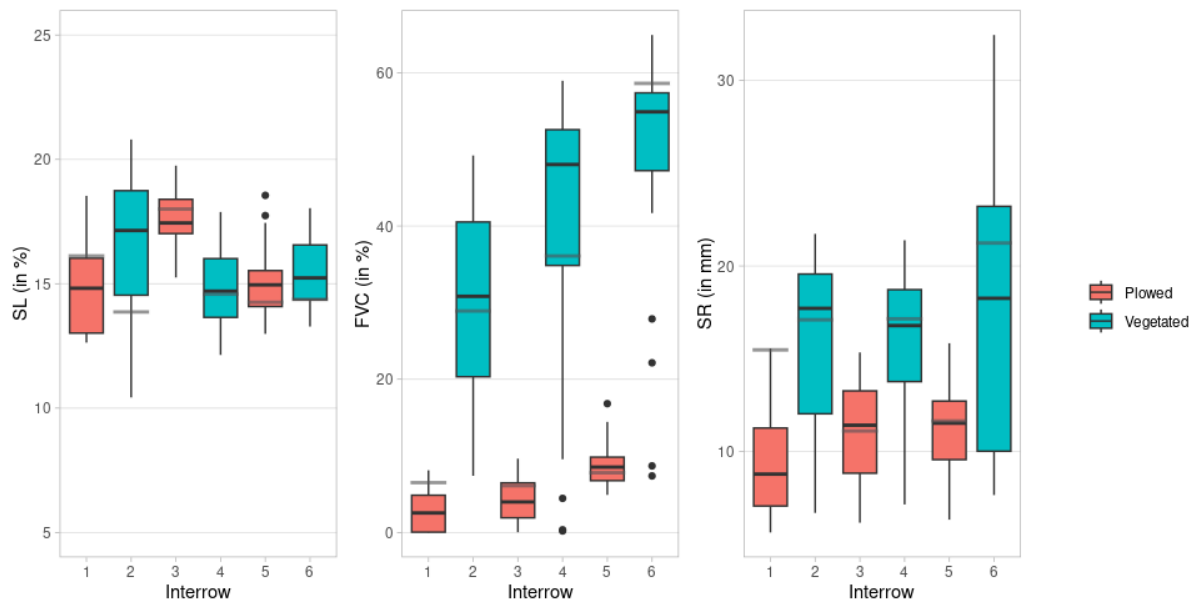


Figure III. 5. Distribution of slope (SL), Fractional Vegetation Cover (FVC), and Surface Roughness (SR) values aggregated by sections for each interrow. Plowed interrows are in red, vegetated interrows are in blue. Values in the deposit zones are shown by gray lines.

3.2. Effect of surface rugosity and mean vegetation cover on unmoved seeds US
 SR, FVC and seed morphology had an effect on US. SR had a positive effect on US, whereas FVC had a negative effect on US . Round seeds were less likely to stay in place than hooked and plumed seeds (Tab. III. 3).

Table III. 3. Estimated coefficient values (+/- standard error SE) associated with factors determining the number of unmoved seeds US. Effects were tested with a generalized linear model with a Poisson distribution, coupled with ANOVA. Significant variables are highlighted in bold characters.

Variable	Estimate (+/- SE)	F	p-value
FVC	-9.4e-4 +/- 4.7e-4	11.93	<0.001
SL	0.005 +/- 0.05	0.0	0.98
SR	5.45 +/- 1.98	5.26	<0.05
Max. discharge	-0.02 +/- 0.01	3.49	0.06
Mass/volume ratio	-0.01 +/- 0.01	0.18	0.65
Seed morphology (hooked as reference)	round seeds : -0.01 +/- 0.01 plumed seeds : NA	3.92	<0.05

3.3. Dispersed seeds

3.3.1. Global effect of soil surface properties on seed dispersal pattern

The section permeability to seed (PS) decreased significantly from low to high values of FVC. PS was lower for high SR values than for low and medium values (Fig. III. 6, Appendix C2). We could not show any significant differences in PS between SL classes.

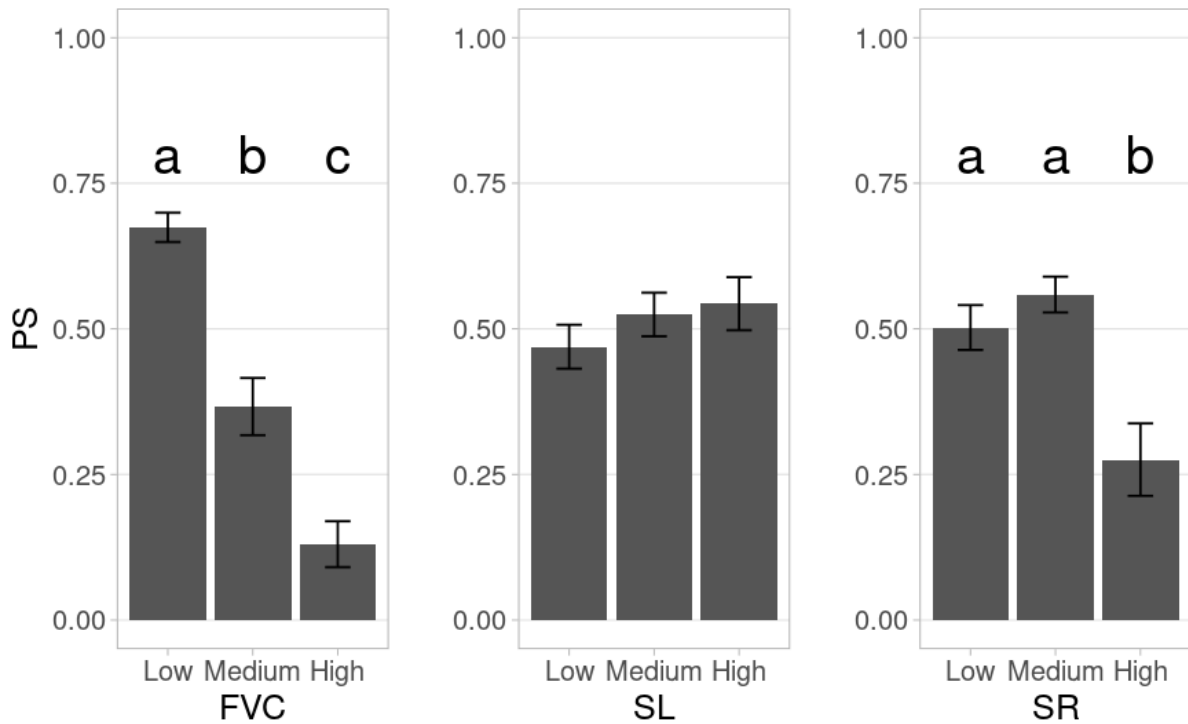


Figure III. 6. Section permeability to seeds (PS) in relation to each class used to test the effect between PS and fractional vegetation cover (FVC), mean slope in the section (SL), and mean surface roughness (SR). Error bars indicate the standard errors associated with the mean PS values. For each graph, different letters indicate significant differences between classes.

3.3.2. Effect of seed morphology on interactions between seed dispersal and soil surface properties

For hooked and plumed seeds, the effect of FVC on PS was similar between medium and high FVC values, while PS decreased significantly from low to high values of FVC (Fig. III.7). The effect of SR on PS was no longer observed for both plumed and hooked seeds, but was still observed for round seeds (Appendix C3).

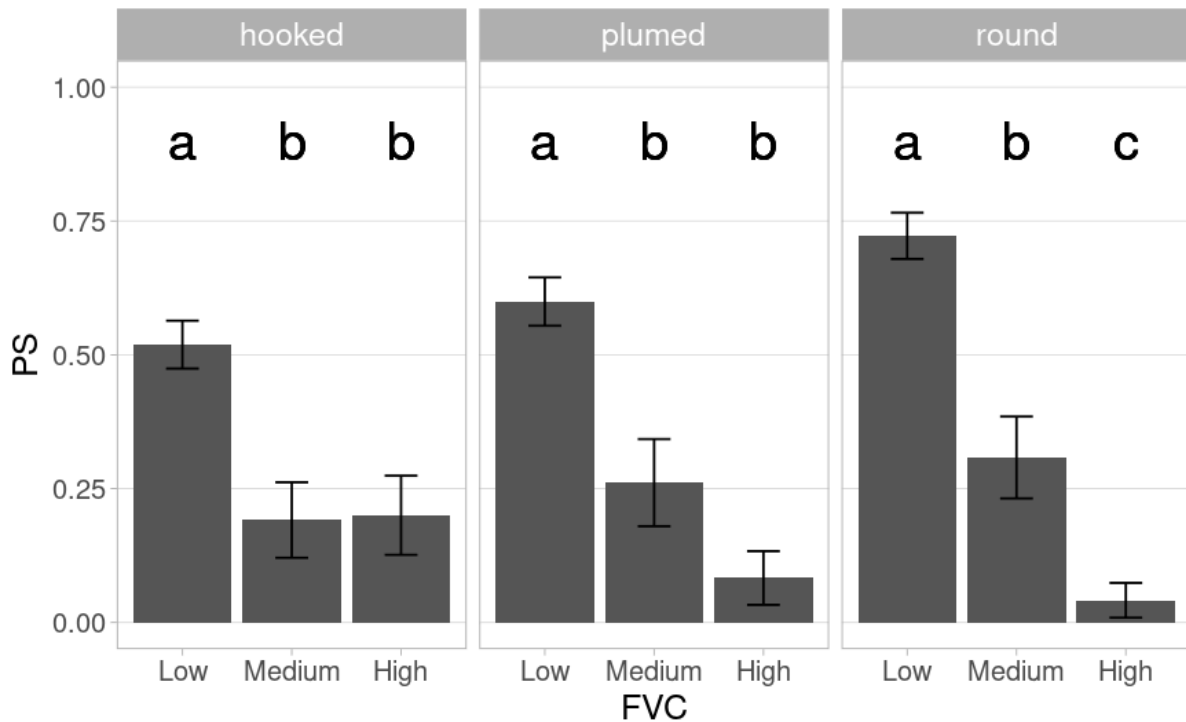


Figure III. 7. Mean section permeability to seeds (PS) in relation to each FVC class, for each seed morphology separately. Error bars indicate the standard errors associated with the mean PS values. For each graph, different letters indicate significant differences between classes.

III. 4. Discussion

4.1. Determinants of absence of dispersal

Surface rugosity (SR) and fractional vegetation cover (FVC) were the main determinants explaining the number of unmoved seeds. While the positive effect of surface rugosity on the number of unmoved seeds is consistent with previous results (Garcia-Fayos et al., 2013), the negative effect of vegetation cover is surprising. Indeed, vegetation has generally been observed to trap seeds during surface runoff (de Rouw et al., 2018), thus we expected to observe a positive effect of FVC on the number of unmoved seeds. However, the negative coefficient value associated with the effect of vegetation cover is extremely low, which refrains us from asserting the vegetation cover actually had a negative effect on seed mobilization. Therefore, in our experiment, the vegetation cover had little effect on the number of unmoved seeds.

No effect of seed density on the number of unmoved seeds (US) was found in our study. Yet seed density is a reliable proxy for buoyancy (Carthey et al., 2016), which is often considered

a facilitating factor for hydrochory (Benvenuti, 2007). In fact, hydrochory in permanent streams also occurs underwater, in the water column, or directly on the streambed (Carthey et al., 2016). Although this process may not be as efficient as surface transport for seed dispersal in permanent water streams, the difference between dispersal at the surface and directly on the streambed may disappear for hydrochory during surface runoff, reducing the importance of buoyancy. In this context, species with non-buoyant seeds (i.e. small poppy, *Papaver rhoeas*) may disperse more easily than in permanent or quasi-permanent watercourses, as suggested by the negative coefficient associated with round seeds on the number of unmoved seeds.

4.2. Effect of soil surface properties on seed dispersal

The first part of our second hypothesis, which expected an effect of soil surface characteristics (modified by agricultural practices) on seed permeability (PS), was partially confirmed. FVC and SR had an effect on seed dispersal, but we could not detect an effect of slope (SL). In other studies, high slope is known to facilitate seed dispersal (Han et al., 2011; Jiao et al., 2011), so it is possible that slope was not contrasted enough in our experimental plot to have a discernible effect on PS. On the other hand, the reduction in PS associated with intermediate to high FVC values is consistent with the well-documented retention of seeds by vegetation, both in streams and rivers (Soomers et al., 2010; Rudi et al., 2018; 2021) and during surface runoff (Bochet, 2015).

The reduction in PS associated with the increase in SR is also consistent with previous studies, as multiple short-distance elevation differences increase seed trapping (Aerts et al., 2006; Isselin-Nondedeu et al., 2006; Soomers et al., 2010).

Regarding the second part of our second hypothesis, as expected, seed morphology influenced the interactions between soil surface characteristics and PS, but not all of them. The lack of difference in PS between medium (25 - 50%) and high (>50%) classes of FVC for hooked *Daucus carota* and plumed *Bothriochloa barbinodis* seeds suggests that seeds with appendages were the most likely to stick to vegetation, which is consistent with a previous study (Bochet, 2015). However, we did not find any difference in the effect of SR and SL on different seed morphologies. If the lack of effect of SL on PS was due to the low contrast between slope values, as we hypothesized earlier, round *Papaver rhoeas* seeds should be more sensitive to slope variations, since their lack of appendages reduces the probability they stick to the soil surface. The fact that the effect of SR persisted only for the analysis based on

round seeds is consistent with this hypothesis, as they rely more on soil surface properties to stop their dispersal than the other two seed morphologies with appendages.

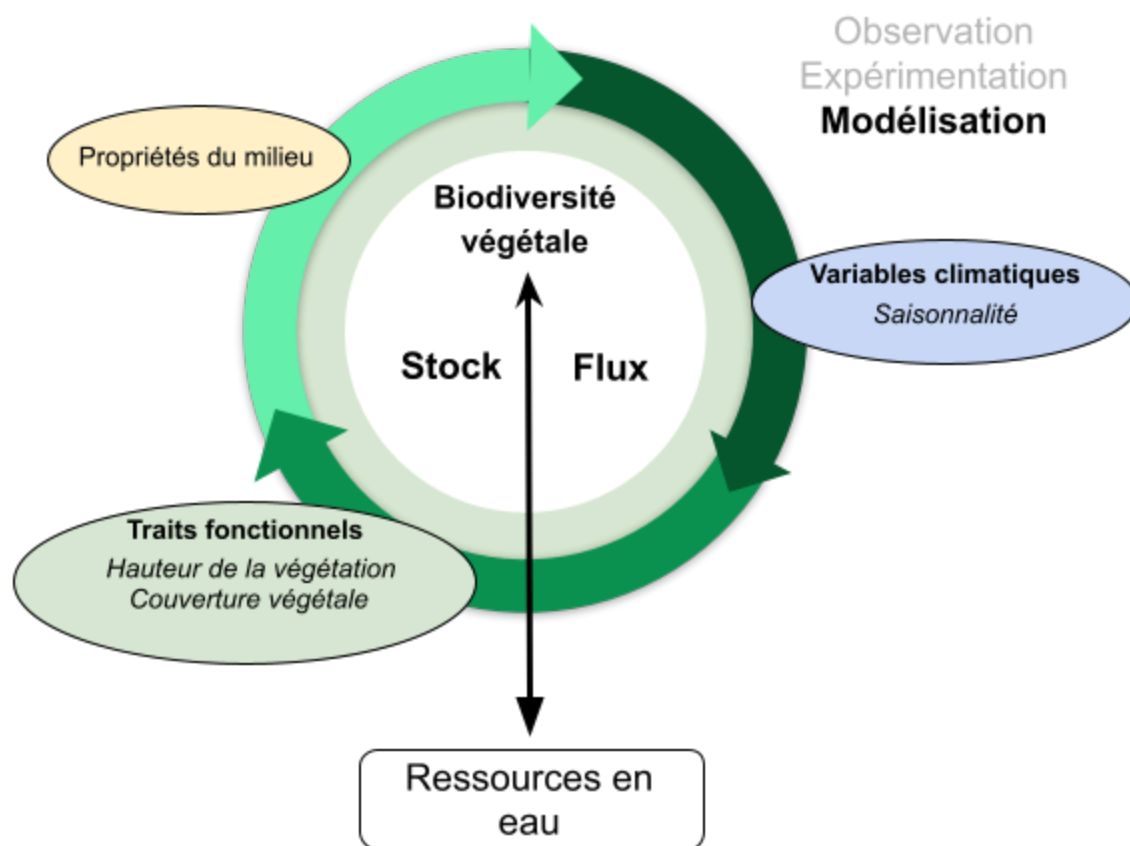
In summary, although plowed interrows have greater permeability to seed dispersal than vegetated interrows, our results suggest that hydrochory may be an important factor in vegetating the bare soil of interrows with spontaneous vegetation during the first year following changes in management practices. The changes in surface properties caused by plowing create seed traps that promote germination and gradual soil cover. Vegetation cover offers numerous advantages over bare soil, especially in Mediterranean climates, as it increases water infiltration, reduces soil erosion, and mitigates air temperature fluctuations (Garcia et al., 2018).

At the end of their dispersal, seeds can integrate the soil seed bank (Faucher et al., 2024), or germinate if environmental conditions are favorable. These processes are of great importance for the spontaneous increase in plant biodiversity (Plue and Cousins, 2018). By providing useful information on the effect of seed morphology on dispersal during runoff, this study may help to develop a modeling approach that combines simulations of vegetation cover growth within vineyard interrows and its effect on the retention of seeds dispersed by hydrochory during surface runoff.

4. 3. Conclusion

This study is the first to investigate the relationship between seed dispersal, soil surface properties, and seed morphology during surface runoff in a Mediterranean agroecosystem. In contrast to similar studies investigating hydrochory during surface runoff (Tekiela and Barney, 2013; Aerts et al., 2006), our study considers seed morphology to provide a more comprehensive understanding of secondary seed dispersal by runoff in terrestrial ecosystems under different soil surface conditions. This information is crucial in the face of climate change, especially for Mediterranean regions and vineyards, as it aids in the development of biodiversity-based mitigation strategies. For example, practitioners could continue to plow their inter-rows to some extent to increase the rugosity of the soil surface, which would promote seed entrapment and establishment and ultimately facilitate the development of a vegetation cover.

Chapitre IV. Modélisation des flux d'eau et de graines



Dans ce dernier axe de la thèse, nous nous sommes intéressés aux interactions eau-végétation à l'aide d'une approche numérique, dans la continuité de l'expérimentation menée sur l'hydrochorie lors de ruissellement de surface, ainsi que du résultat issu de la caractérisation de la banque de graines du sol ayant observé une part plus importante d'espèces hydrochores au sein des fossés agricoles situés dans un paysage marqué par des pratiques extensives. À l'aide d'un modèle de croissance végétale construit grâce à l'agrégation et l'adaptation de modèles déjà établis, nous avons exploré l'influence du changement climatique sur l'évolution des interactions eau-végétation, caractérisées par la friction générée par le couvert végétal sur les écoulements d'eau, ainsi que par l'estimation de la proportion de graines retenues par la végétation.

Le chapitre qui suit a été rédigé sous la forme d'un article, en préparation d'une soumission à la revue *Ecological Modelling*.

IV. 1. Introduction

Water flowing through a vegetation cover is affected by it, and the metric associated with the effect of vegetation on water flows is referred to as friction. Friction plays an important role in Mediterranean agrosystems, both by its presence or its absence. The ecosystem services provided by vegetation for runoff and associated soil erosion mitigation are well established (Busico et al., 2023; Lal et al., 2020; Wu et al., 2020), as well as its capacity to trap seeds (Vinatier et al., 2017 ; Rudi et al., 2021), and other particles such as pesticides residues (Dollinger et al., 2015).

Friction is determined by the individual architecture of each plant, and the configuration of the plant community (Nepf, 2012). At the individual level, traits such as plant height, leaf area, and ground surface covered by the plant are the major determinants of friction (Rudi et al., 2021; Wang et al., 2019). Then, the density of individuals forming the plant community, and its relative importance considering the volume containing the water flow also influence the overall friction generated (Green, 2005).

Seed retention is a consequence of friction, and defines the temporary or permanent trapping of seeds, each with its own specificity (Chambert & James, 2009; Defina & Peruzzo, 2010). Seed retention is an important determinant of seed dispersal inside agricultural waterways (Greet et al., 2012; Hyslop & Trowsdale, 2012). More precisely, seed retention is associated with the plant community maintenance and diversification of those waterways (Fryirs & Carthey, 2022; Su et al., 2022).

In the Mediterranean basin, rainfall will become more scarce and intense due to climate change during the next decades, thus increasing the intensity of runoff events and their probability to cause soil erosion, flooding, as well as increasing the frequency of droughts (Cozannet et al., 2022; Busico et al., 2023). As vineyards are the main agriculture in the Mediterranean, droughts are threatening the wine production, especially in a context where water stress is already perceived as a threat (Garcia et al., 2018).

Climate change in the Mediterranean also threatens agrosystems as a whole, and increasing the biodiversity (i.e., biodiversification) is a strategy increasingly put forward to prepare these landscapes (Garibaldi et al., 2021; Jeanneret et al., 2021). Seed circulation facilitates the promotion of biodiversity (Plue & Cousins, 2018), linking friction and seed retention to the biodiversification effort.

Nonetheless, Mediterranean vineyards are typically combined with dense ditches networks created to mitigate soil erosion by collecting runoff water (Levavasseur et al., 2014;

2015), which requires frequent vegetation removal to maintain their purpose (Vinatier et al., 2017). Additionally, the vegetation inside inter-rows is actively managed to avoid competition for water between the vegetation cover and the vine (Fernandez-Mena et al., 2021; Delpuech & Metay, 2018; Garcia et al., 2018; Celette et al., 2010). Thus a trade-off arises between biodiversification and the management of water resources for inter-rows and ditches inside Mediterranean vineyards.

Modeling approaches of various scenarios built on climate forecasts seem better suited than experimental studies to help anticipate these outcomes because they allow for exploring the range of possibilities (Naulleau et al., 2022; Joly et al., 2021). In the Mediterranean context, simulations inside agricultural ditches and vineyards' inter-rows would provide insights on the evolution of vegetation-water interactions under climate change.

Such simulations would require modeling a plurispecific vegetation cover, with access to the specific traits related to vegetation friction and seed retention. Models of vegetation growth exist (Colbach et al., 2021; Courault et al., 2021; Celette et al., 2010), as well as models describing vegetation friction and seed retention (Rudi et al., 2022; Nepf, 2012), but none aggregates both components.

Consequently, using the insights from those models could contribute to developing a vegetation growth model destined to water-vegetation interactions in inter-rows and ditches of Mediterranean vineyards. Then, simultaneous information on service provision and quantitative results on possible trade-offs between runoff mitigation and seed retention could be obtained.

This paper describes MoVeGrowth, a model built on previously established formalisms to simulate vegetation friction and seed retention in Mediterranean agrosystems, focusing on both the vineyard inter-rows and the typical agricultural ditches adjacent to vineyards. After a description of the calibration and evaluation procedures performed, results from a simple case study on the evolution of vegetation cover, water friction, and seed retention under rising air temperatures are presented.

IV. 2. Material and Methods

MoVeGrowth simulates a fixed number of species, chosen by the user before each simulation. The pool of potential species was determined using vegetation surveys conducted in various Mediterranean vineyards, both from the literature (Fried et al., 2019; Rudi et al., 2018), and

from the vegetation surveys conducted in the Roujan catchment (south of France), which were used for calibration and evaluation of the model.

2. 1. Presentation of the model

- **Conceptual basis**

Aspects of vegetation growth and senescence are derived from Duru et al. (2009), with the adaptations related to the addition of hydrological aspects as included in the WaLIS model (Celette et al., 2010), and germination is based on the hydrothermal time theory from Gummerson (adapted by Paré, 2011, from Gummerson, (1986)). In addition to the computation of water friction and seed retention, MoVeGrowth differentiates itself from the models it was based on by the possibility to simulate a plurispecific plant community, as well as allowing for the simulation of a plant community inside a ditch. The model revolves around the subdivision of species into cohorts throughout the simulation. Cohorts correspond to a monospecific group of individuals identified by the day they germinated.

- **Process overview**

The model works on a daily basis, and consists of repeating operations on loop until the end of the simulation is reached. The first operations of a loop are always the same and consist of updating the variables depending on daily climate and/or the existing plant community (i.e., the water balance, sum of temperatures, sum of rainfall, etc.), then computing the effect of these changes on vegetation (i.e., dormancy break, germination, growth, senescence). As said earlier, the leaf area is used as a proxy for the overall vegetation growth (Celette et al., 2010). Thus, after computing the new daily leaf area, the model calculates the corresponding values for a variety of species-level traits, such as vegetation height, cover, and dry masses. Then, the last steps of a loop corresponds to the calculation of community-level traits such as the total leaf area, the total vegetation cover, the proportion of seeds potentially retained by vegetation, and the potential friction against water flows (Fig. IV.1).

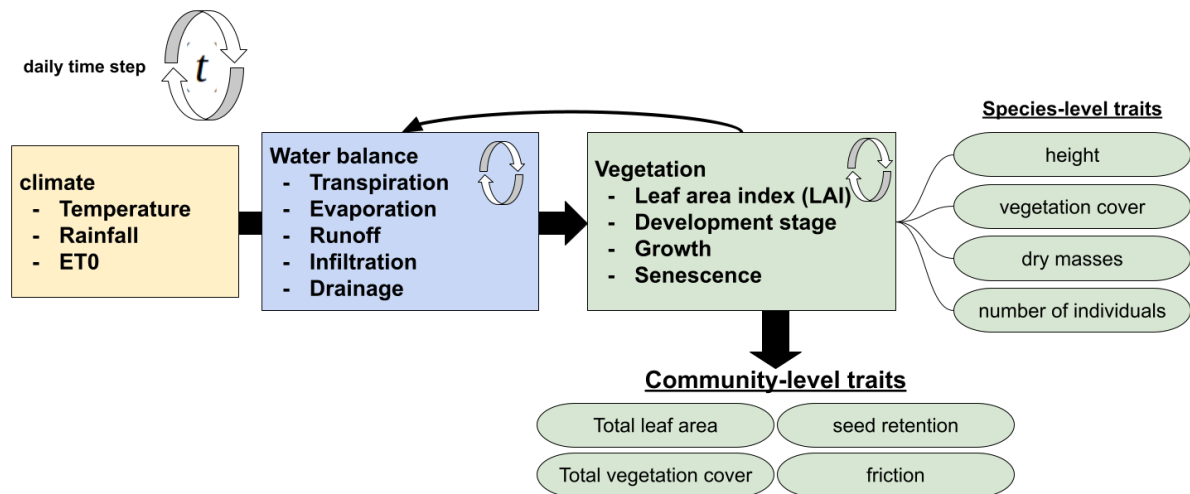


Figure IV.1. Conceptual representation of the model functioning.

The starting time of the simulation is determined by the first entry in the climate dataset associated with each simulation scenario. The starting point of the model is a bare soil surface, with no prior history on previous treatments, rainfall, or species assemblage. Thus, there are no cohorts at the beginning of the simulation, only the species with all state variables set to 0 or a fixed number of the relevant variables (i.e. number of seeds, dormancy, ...). All sums of temperature, soil moisture and rainfall are also set to 0. Other initialization values will only vary between simulation scenarios, in accordance with the pedoclimatic data and calendar of practices collected.

2. 2. Relevant equations

Only the parts related to traits included in the calibration or evaluation procedures, as well as those related to vegetation friction and seed retention will be detailed hereafter (see Appendix F for a complete description of the functions in the model).

- Species-level traits

Vegetation growth is based on an equation presented in Duru et al. (2009) for an herbaceous plant cover, adapted by Celette et al. (2010) for vineyards. The daily growth $GLAI$ (in $m^2.m^{-2}$) is computed using pre-existing leaf dry mass DW_{leaf} (in $g.g^{-1}$), daily mean temperature T (in $^{\circ}C$), an index of water stress named WI , and a specific daily growth rate LAI_{rate} . A coefficient of soil nitrogen availability NNI is also included, it will be constant

during all simulations, and set at 0.3, the value provided for the use of WaLIS in Mediterranean soils (Eq. 1, Celette et al. 2010). The value of LAI_{rate} was first estimated using information about species traits available in the literature. The estimation of the LAI_{rate} led to scaling differences with experimental data in the first simulation runs, thus a coefficient was added to adjust the growth rate equally over every species, and will be calibrated using experimental data. The value of WI corresponds to the ratio between the simulated transpiration value and the threshold transpiration value under which water stress begins, with values ranging from 0 when the water stress is highest, to 1 when the water is not the limiting factor to vegetation growth.

$$GLAI_j^i(t) = LAI_{rate}^i * DW_{leaf\ j}^i(t - 1) * 1,71 \cdot 10^{-3} * T(t)^2 * WI^i(t) * NNI$$

t the day of simulation, i the species, j the cohort rank (Eq. 1)

Leaf senescence is triggered by reaching a fixed sum of temperatures (LLS , in °C.days), and is calculated based on the leaf area index at the time of computation, the sum of temperatures since the germination of the cohort (STT , in °C.days), and the threshold value of sum of temperatures marking the beginning of the senescence stage LLS (Eq. 4). This computation is similar to previous models (Schaphoff et al., 2018), and is associated with a dimensionless parameter k_s governing the slope of the relationship. k_s will be calibrated following the protocol described further in this article.

$$SLAI(t)_j^i = LAI(t - 1)_j^i * \frac{k_s}{\frac{STT_j^i}{LLS^i}} \quad (\text{Eq. 2})$$

Dry weight partitioning evolves during the development of the vegetation, in order to reflect the shift in resources allocation as the cohort ages. The leaf dry weight DW_{leaf} (in kg.m⁻²) is calculated as the ratio between the cohort LAI and the leaf area ratio LAR , the conversion coefficient between leaf area and global plant mass (in m².kg⁻¹, Eq. 3). LAR is a trait measured in the literature, for each species included in the model the TRY database (Kattge et al., 2020) was queried, and the closest value based on APG-III phylogenetic classification was used in the model (Angiosperm Phylogeny Group, 2009).

$$DWleaf_j^i(t) = LAI_j^i(t) / LAR^i \text{ (Eq. 3)}$$

Then, cohort height H (in m) is calculated from the overall dry mass DW_{tot} multiplied by two coefficients, DW_H1 and DW_H2 , which were extracted from the TRY database (Kattge et al., 2020; Eq. 4).

$$\sum_1^i \sum_1^j H_j^i(t) = DW_{H1}^i * DW_j^i(t)^{DW_{H2}^i} \text{ (Eq. 4)}$$

- Community-level traits

The total surface vegetation cover and the global leaf area are calculated as aggregative variables to have a meaningful outlook on the simulated plant community. The total leaf area is calculated as the sum of leaf area index for each species, multiplied by the number of individual plants and the ground surface covered by one individual plant (Eq. 5).

$$LA_{TOT}(t) = \sum_1^i \sum_1^j LAI_j^i(t) * n(plants)_j^i * surface\ of\ 1\ plant^i \text{ (Eq. 5)}$$

Then, the percentage of surface covered by vegetation (VC) is determined from an exponential relationship with LA_{TOT} multiplied by kVC , a conversion coefficient which will be determined following the calibration procedure (Eq. 6).

$$VC(t) = 1 - exp^{-kVC * LA_{TOT}} \text{ (Eq. 6)}$$

To calculate the effect of vegetation on water friction, the vegetation frontal area per volume a_f (L^{-1}) is calculated for each species (Equation 6). To facilitate the calculation, the effect of each cohort is assumed to be similar to a regular trapezoid facing the water flow, with the width of the upper base L_{sup} equal to the number of individuals in the cohorts multiplied by the area covered by an individual *groundcover* and the percentage of area covered by vegetation. The width of the lower base L_{inf} is derived from L_{SUP} using a dimensionless coefficient k_{shape} set to 2 (Eq. 7). For the calculation of the seed retention factor, vegetation at the water surface is considered to be contained within a circle of diameter L_{SUP} (Fig. IV.2).

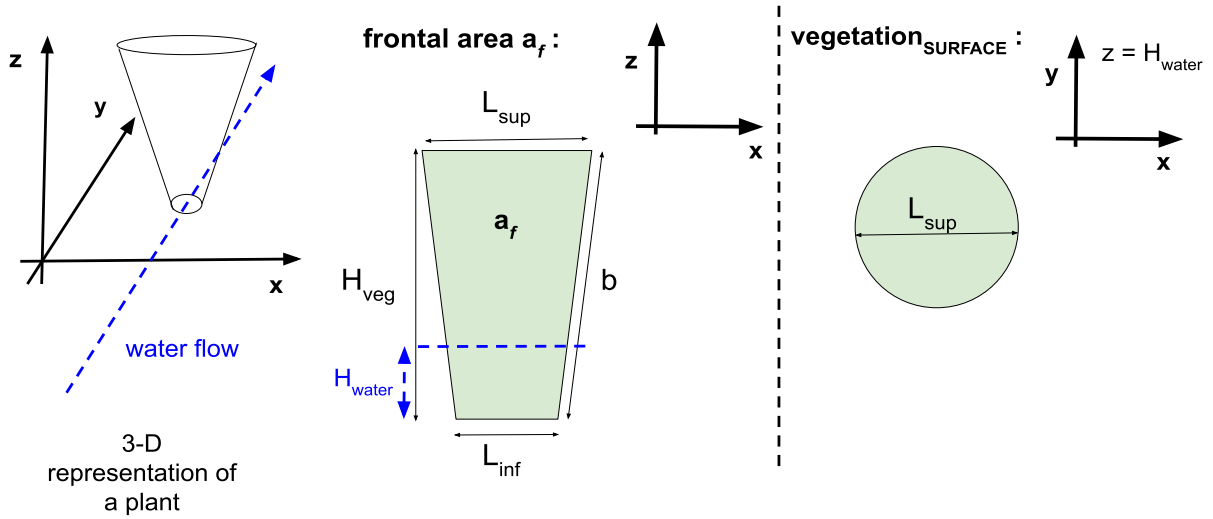


Figure IV.2. Theoretical representations of the vegetation for the calculation of the frontal area a_f , and the surface of vegetation situated at water level noted $vegetation_{SURFACE}$.

$$a_f^i(t) = 0.5 * \left(L_{sup_j}^i(t) + L_{inf_j}^i(t) \right) * b_j^i(t) \quad (\text{Eq. 7})$$

The water friction can be derived from this vegetation metric in interaction with the water level by calculating the Manning coefficient K_{man} (dimensionless, Nepf, 2012). When the mean height of the vegetation cover is equal to or higher than the water level, K_{man} varies as a_f and H_{WATER} , in conjunction with the constant drag coefficient C_D and the gravitational force g (Eq. 8). Then, when the vegetation is submerged, K_{man} is also determined by the shear stress coefficient C_x (dimensionless, varying between 0.05-0.13 in field data according to Luhar and Nepf, 2011) and the blockage factor B , which is the ratio of a_f to the total frontal area (Eq. 9). Both equations include the constant K , equal to $1 \text{ m}^{1/3} \cdot \text{s}^{-1}$, which is required to make the equations dimensionally correct.

$$\text{if } H_{water}/H_{veg} \leq 1: 1/K_{man} = \left(0.5 C_D * a_f * H_{water} \right)^{0.5} * \frac{K \cdot H_{water}^{1/6}}{g^{0.5}} \quad (\text{Eq. 8})$$

$$\text{if } H_{water}/H_{veg} > 1: 1/K_{man} = \left[\left(2/C_x \right)^{0.5} * (1 - B)^{-1.5} + \left(\frac{2}{C_D \cdot a_f \cdot H_{veg}} \right)^{0.5} * B \right] * \frac{K \cdot H_{water}^{1/6}}{g^{0.5}} \quad (\text{Eq. 9})$$

Seed retention by vegetation can be determined using the surface of vegetation at the water level, noted $vegetation_{SURF}$ (in m²), coupled with the frontal area a_f , the Reynolds number \mathcal{R} (dimensionless), and the length of the section over which water flows l (Eq. 10; Rudi et al., 2021).

$$seed\ retention(t) = 1 - \exp^{\frac{-vegetation_{surf}}{a_f(t) \cdot \mathcal{R} \cdot 10^{-5} \cdot l}} \in [0; 1] \text{ (Eq. 10)}$$

In addition to mowing, which was already present in WaLIS, 5 other types of practices can be simulated : eco-burning, mowing, chemical weeding, tillage, and dredging. All of them decrease the vegetation cover with varying intensities, except the application of a pre-emergence herbicide treatment.

2. 3. Simulation context

- Study site

The Roujan catchment (43°30'N, 3°19'E) is situated west of Montpellier, France. This catchment is a part of the long-term observatory ORE-OMERE, and has thus been continuously monitored for more than 30 years (Molénat et al., 2018). The Roujan catchment area is a small catchment area (<1 km²) mostly occupied by vineyards framed by a network of drainage ditches dug by stakeholders to drain some of the water from the soil, collect runoff and limit erosion. The catchment is characterized by a sub-Mediterranean subhumid climate with a long dry period, and the majority of rainfall occurs in spring and autumn. The average rainfall is 600 mm.year⁻¹ (Molénat et al., 2018). The vineyards that constitute most of the Roujan catchment area belong to different vinegrowers. The maintenance of the drainage ditches is the responsibility of the owners of the neighboring vineyards and typically consists of removing the vegetation by mowing or burning the vegetation to preserve the water flow capacity. More rarely, dredging/chemical weeding operations are carried out.

- Vegetation surveys description

Three separate campaigns of vegetation surveys were used. The first one has been conducted from 2015 to 2016, as part of a study aiming to track the evolution of ditches' properties in

response to 5 different management practices. This study was conducted in the ditch situated downstream from the outlet of the Roujan catchment. For each management practice, vegetation cover and maximal height were measured 19 times on separate sections of the same ditch (i.e., 95 separate values; for a detailed description, see Dollinger et al., 2017). The second survey was conducted on inter-rows of 6 different vineyard plots in 2019, to track changes in surface state variables following mowing procedures conducted in the field. Vegetation cover and mean height were measured 12 times. Lastly, the third survey was conducted in 7 ditches of the ditch network of the Roujan catchment, from February to August, in 2022 and 2023. During this survey, the vegetation cover was estimated 14 times over 7 quadrats (50x50cm) and averaged (i.e., 98 separate values).

2. 4. Model calibration and evaluation

The first dataset campaign was used in the evaluation of the model. Half of the second dataset (i.e. 36 values) was used in the calibration dataset, and the other half was used in the evaluation dataset. Each value of this dataset corresponds to a vegetation height and cover measurement. The third dataset was used for the calibration of the model (Fig. IV.3). To summarize, 134 values were used for calibration, and 131 for evaluation.

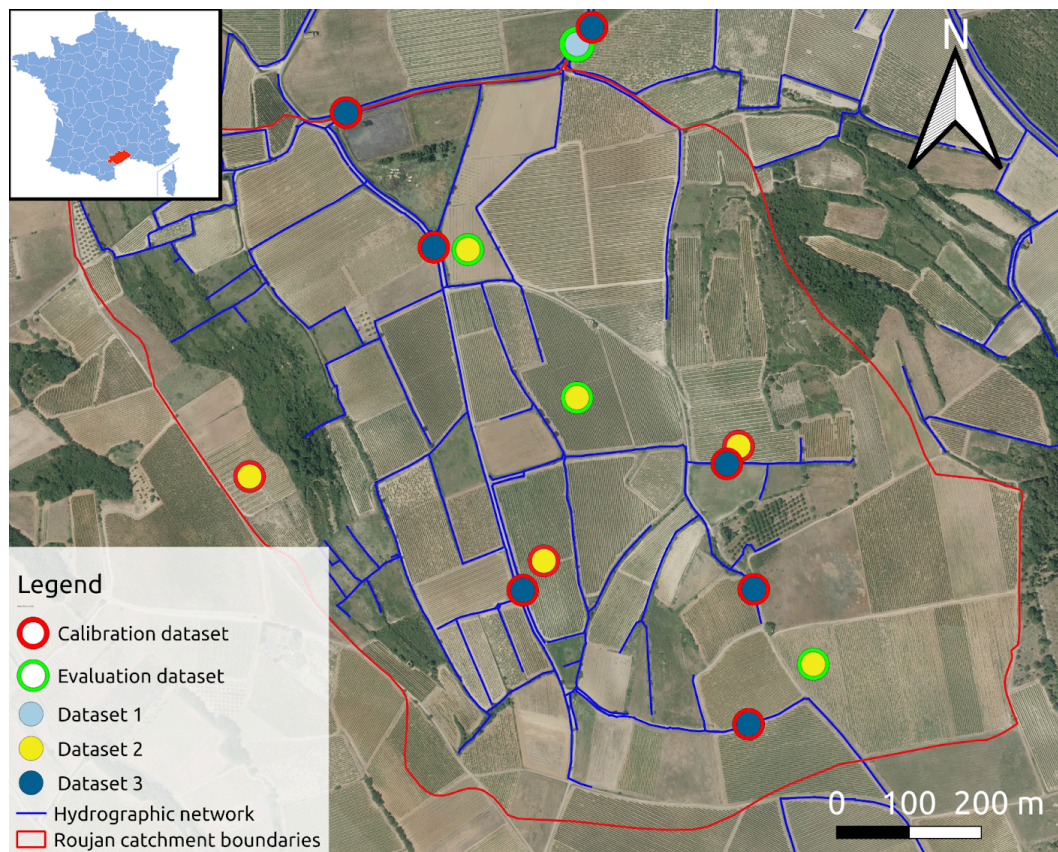


Figure IV. 3. Localization of the vegetation surveys used for the calibration and validation procedure, located in the Roujan catchment (43°30'N, 3°19'E). The northeast point corresponds to the catchment outlet.

- **Model calibration**

Calibration was conducted on three parameters, LAI_{RATE} , k_{VC} , and k_{SEN} , respectively associated with the vegetation growth, the conversion from LAI to vegetation cover, and senescence. Calibration was performed by finding the set of values for these parameters minimizing the relative root mean squared error (RRMSE, Eq. 11) value between the predicted value and its corresponding observed value. Both community-level vegetation cover and height were used. The L-BFGS-B optimization method (Byrd et al., 1995) was chosen for its low computation time. LAI_{RATE} and k_{SEN} were both constrained to be a value between 0 and 1, and k_{VC} was constrained to be a value between 1 and 3. Simulations were set up to start 6 months prior to the first calibration values of vegetation height or vegetation cover. To reflect the differences between inter-rows and ditches, two separate calibration procedures were performed (Tab. 1).

$$RRMSE = \sqrt{\frac{\frac{1}{n} \sum_i^n (y_i - \hat{y}_i)^2}{\sum_i^n (\hat{y}_i)^2}}$$

y_i the observed values, \hat{y}_i the simulated values (Eq. 11)

Table IV. 1. Results of the calibration procedures performed on LAI_{RATE} , k_{SEN} , and k_{VC} , respectively associated with the vegetation growth, senescence, and the conversion from LAI to vegetation cover

	LAI_{RATE}	k_{SEN}	k_{VC}
Inter-rows	0.09	0.19	4.49
Ditches	0.18	0.01	5

- **Model evaluation**

To evaluate the performance of the model calibration, and estimate the relative bias between simulated values and observed values, RRMSE and percent bias (p-bias, Eq. 12) values were calculated between simulated and experimental values. For inter-rows, vegetation cover and vegetation height were simulated with a RRMSE of 18.5% and 20.6%, and p-bias values equal to -23.2% and -58.7%.

For ditches, vegetation cover and vegetation height were simulated with a RRMSE of 9% and 9.1%, and p-bias values equal to -15.6% and 34%. Overall MoVeGrowth performs better on ditches, especially vegetation cover prediction, while inter-rows simulations underestimate the vegetation traits (Fig. IV.4).

$$p - bias = 100 * \frac{\sum_i^n (\hat{y}_i - y_i)}{\sum_i^n (y_i)}$$

y_i the observed values, \hat{y}_i the simulated values (Eq. 12)

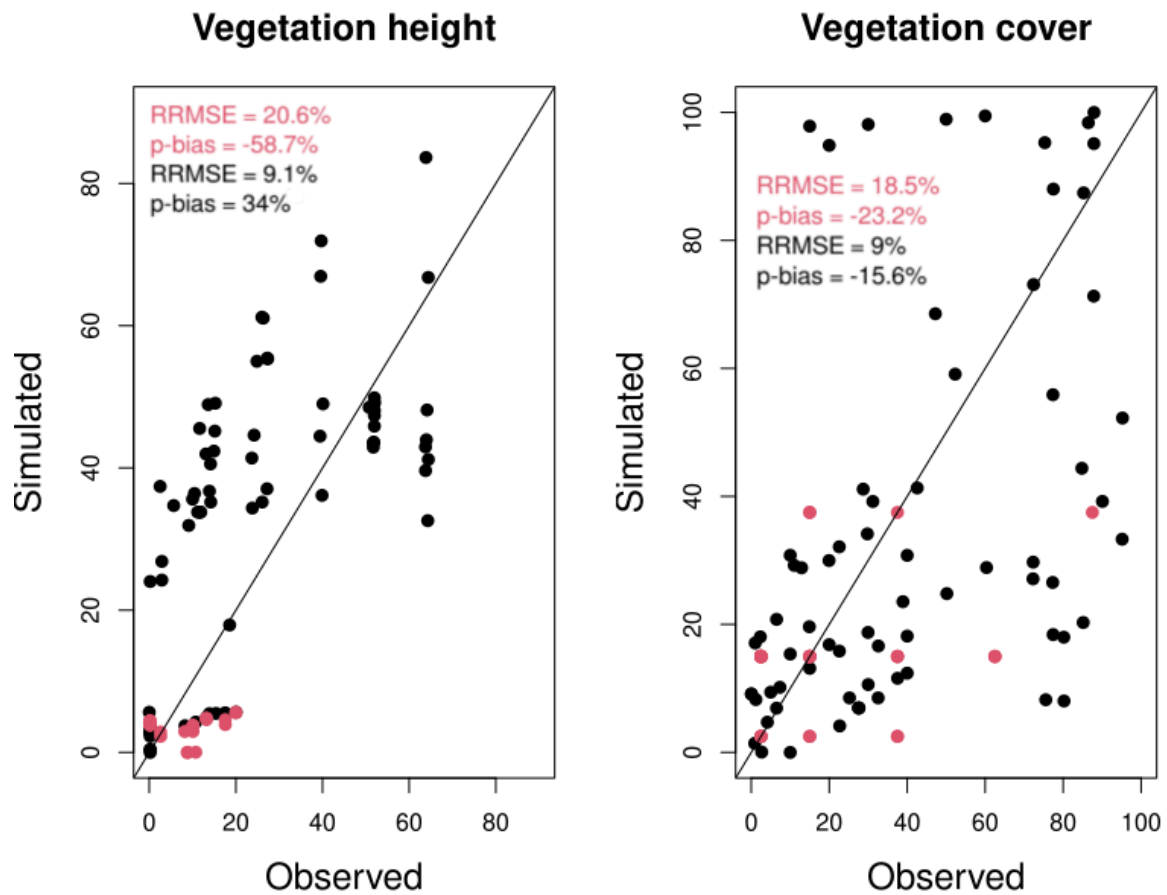


Figure IV. 4. Simulated versus observed vegetation height (left) and vegetation cover (right) for ditch (in black, $n = 71$) and inter-rows (in red, $n = 36$) simulations. RRMSE and percent-bias values are given for inter-rows and ditches separately, with the same color attribution than the points.

Additionally, the water-balance was compared to the values used for the evaluation of WaLIS on Mediterranean vineyards. The RRMSE between observed values and values produced by the model was around 1% (Appendix D).

2. 5. Case study

- Simulation plans

To explore the projected evolution of the vegetation-water cycle interaction, the average water friction generated by the simulated vegetation cover during runoff and/or flood events, as well as the seed retention by the vegetation, were compared between current climate and future meteorological scenarios. Records from the Roujan catchment, where the data used for calibration and evaluation were collected, were used to build these scenarios. More specifically, records from 2013 to 2023 were used to represent the current climate, and

climate change scenarios were based on the same records with gradual increments in daily air temperature. The increments in daily mean air temperature ranged from +0.5°C to +4°C. The +4°C limit was chosen to reflect the approximate increase in mean annual air temperature projected between 2013 and 2100 for the Roujan catchment, under the Representative Concentration Pathway 8.5 (referred to as RCP8.5), released by the IPCC in 2019. The RCP8.5 is thought to describe the climate under a global increase in atmospheric carbon dioxide in a business-as-usual scenario, coupled with the absence of effective climate policies (Fig. IV. 5). In addition to the scenarios constructed by the fixed temperature increase, the projected climate from 2090 to 2100 derived from RCP8.5 was also included to have a realistic climate scenario. This scenario will be referred to as the RCP 8.5 scenario.

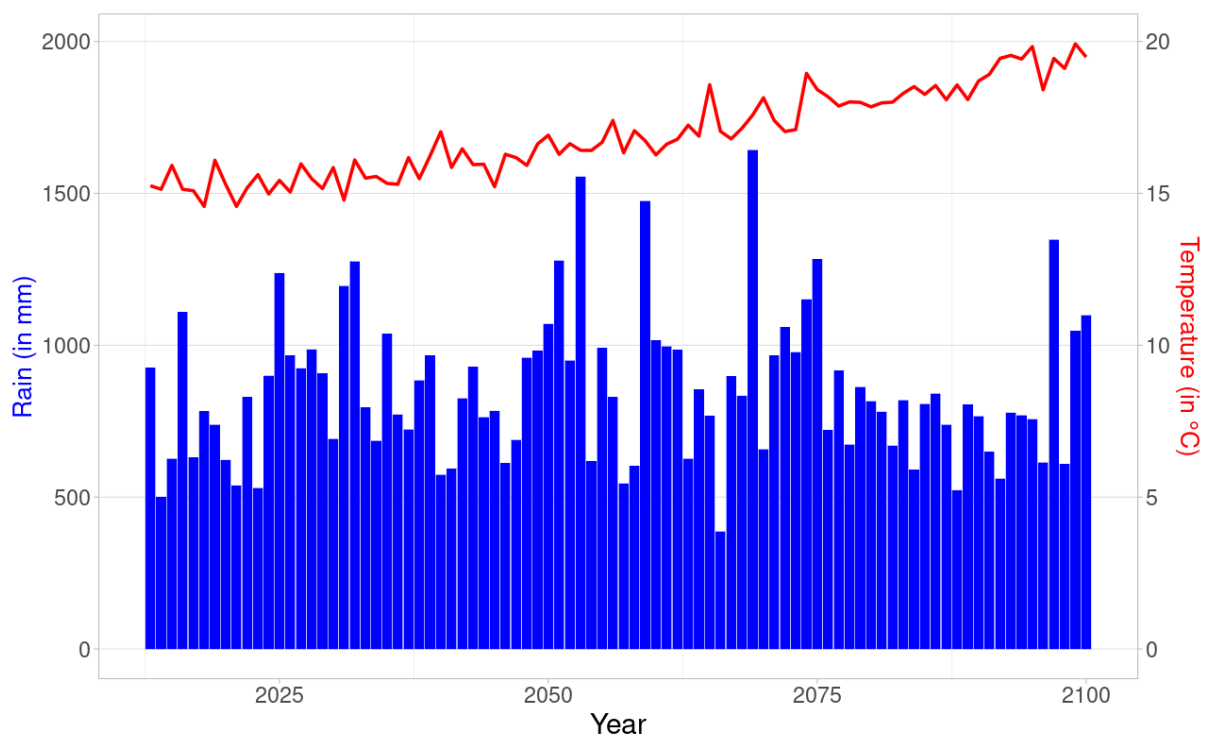


Figure IV. 5. Annual rainfall (in blue, in millimeters) and mean air temperature (in red) from 2013 to 2100, as predicted by the ALADIN regional climate model for the meteorological station closest to the Roujan catchment (Pouzolles meteorological station, GPS : 43.49500, 3.27539), where the data used for the calibration and evaluation were collected.

Then, the model was run for every scenario (i.e., +0°C / +0.5°C / +1°C / +1.5°C / +2°C / +2.5°C / +3°C / +3.5°C / +4°C, and RCP 8.5), for both ditch and vineyard inter-row situations. The evolution of vegetation-water interactions will be tracked by calculating the water friction and the seed retention during each simulation.

Both the water friction and the seed retention calculation require a non-zero value of water level, thus their respective functions were run with theoretical values of water level. In consequence, simulations will produce potential values for the two variables. This also implies that upstream water flows will not be considered. Water level was set as the ditch depth (i.e., 0.8m) for ditch simulations, and 0.05m for inter-rows simulations, based on field observations.

- **Statistical analysis**

Statistical analyses were performed using R v.4.3.1. The vegetation cover, water friction and seed retention values obtained for each date were averaged over all the years, for inter-rows and ditch simulations separately. Then, the relative change between the values obtained for the control scenario (+0°C) and the value obtained for each scenario was calculated. The resulting values were not normally distributed for both types of simulation, thus the effect of the elevation in temperature on the relative change of vegetation cover, water friction and seed retention values was tested by calculating the Spearman's rank correlation coefficient between these variables and the rise in temperature. Then, the differences between each level of temperature rise was tested by performing pairwise Wilcoxon tests.

IV. 3. Results

Only the correlation coefficient between the relative change in vegetation cover and the scenarios produced by ditch simulations was significantly negative. (inter-row : $\rho = 0.01$, $p = 0.54$; ditch : $\rho = 0.67$, $p < 0.001$; Fig. IV. 6). In addition, the relative change in vegetation cover was different between the control scenario and scenarios with a 0.5°C rise and higher, as well as between scenarios between a 0.5 and 1.5°C rise and higher. From the +2°C scenario onwards, scenarios with a 0.5°C difference were no longer different.

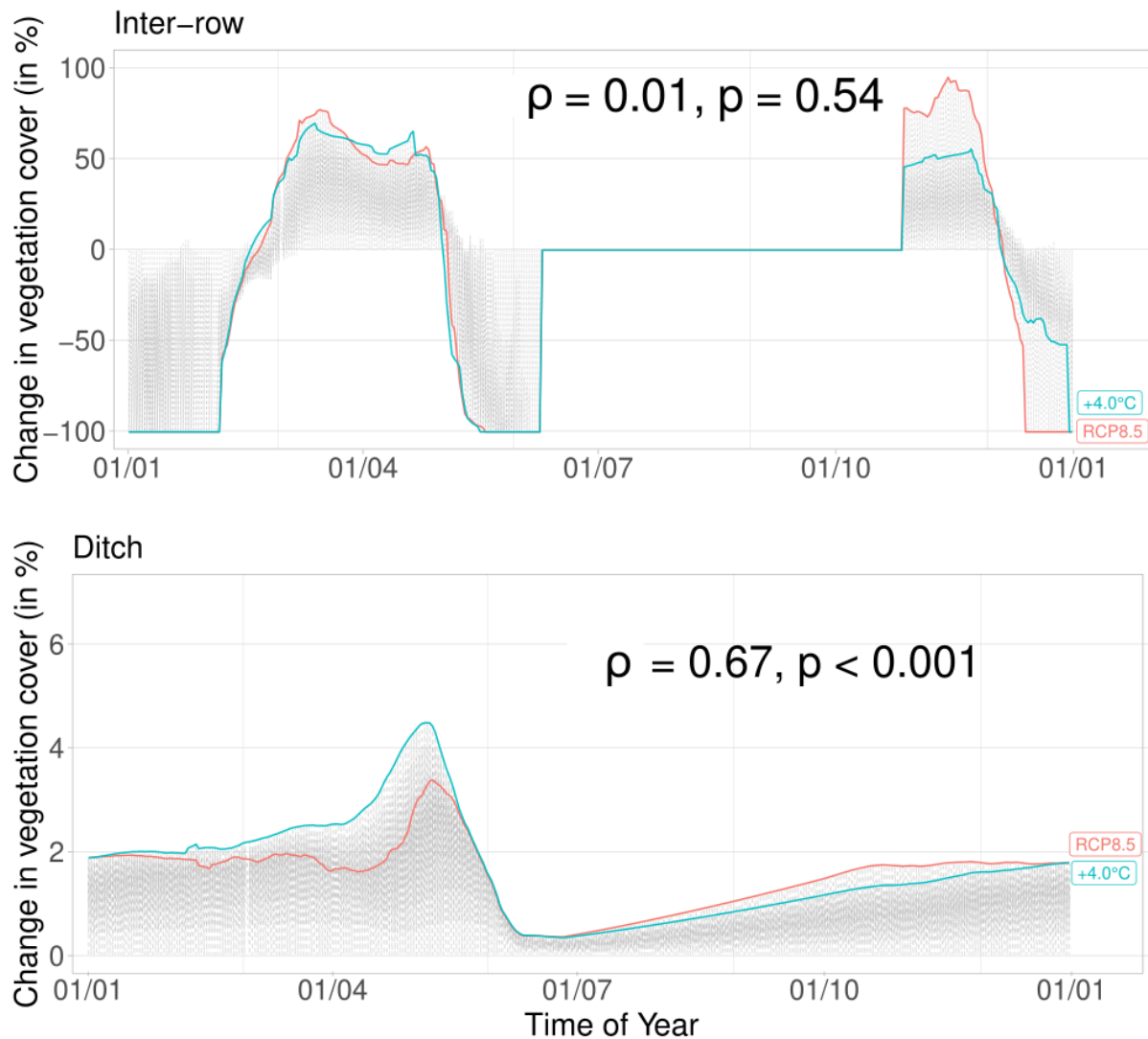


Figure IV. 6. Evolution of the change in vegetation cover values aggregated over 10 years of simulation relative to the control (i.e. +0°C) scenario. Simulations produced by the +4°C and RCP 8.5 scenarios are highlighted in blue and red respectively. Other simulations are displayed in gray dotted lines.

Both correlation coefficients between the scenario and the relative change in water friction were negative (inter-row : $\rho = -0.05, p < 0.001$; ditch : $\rho = -0.92, p < 0.001$; Fig. IV. 7). For inter-rows simulations, the relative change in water friction was significantly different between the control scenario (i.e. +0°C) and scenarios with a 3°C and higher rise (Fig. IV. 7). In ditches simulations, the relative change in water friction was different between all scenarios.

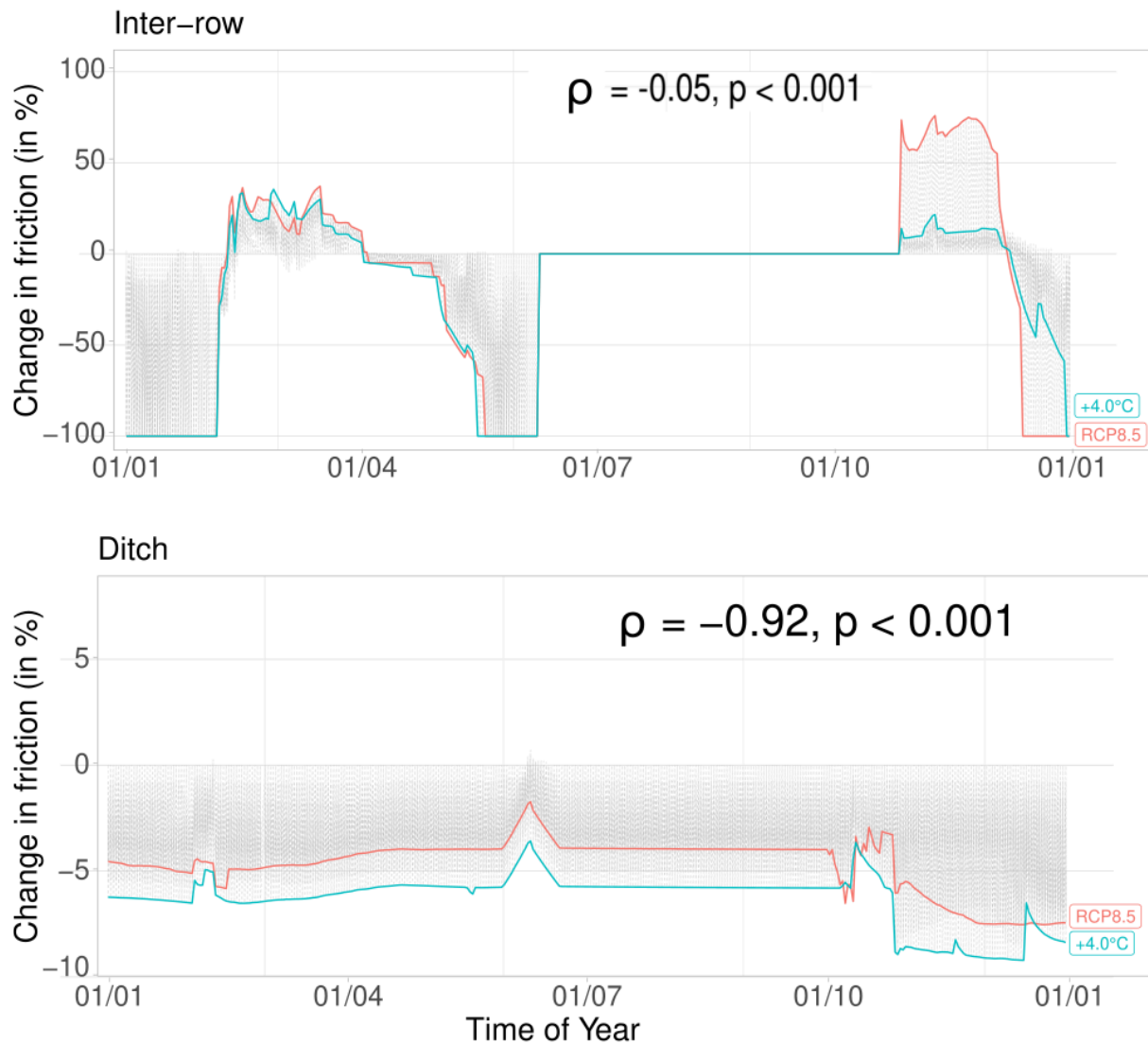


Figure IV. 7. Evolution of the change in water friction values aggregated over 10 years of simulation relative to the control (i.e. +0°C) scenario. Simulations produced by the +4°C and RCP 8.5 scenarios are highlighted in blue and red respectively. Other simulations are displayed in grey dotted lines.

The correlation coefficients between the scenario and the relative change in seed retention were both significant. The correlation was negative for inter-rows ($\rho = -0.04, p < 0.001$), and positive for ditches ($\rho = 0.43, p < 0.001$; Fig. IV. 8). For inter-rows simulations, the seed retention was only significantly different between the control scenario (i.e. +0°C) and the scenario with a 0.5 and 1°C rise. For ditch simulations, the seed retention was significantly different between all scenarios except between the control scenario and the RCP 8.5 scenario (Fig. IV. 8).

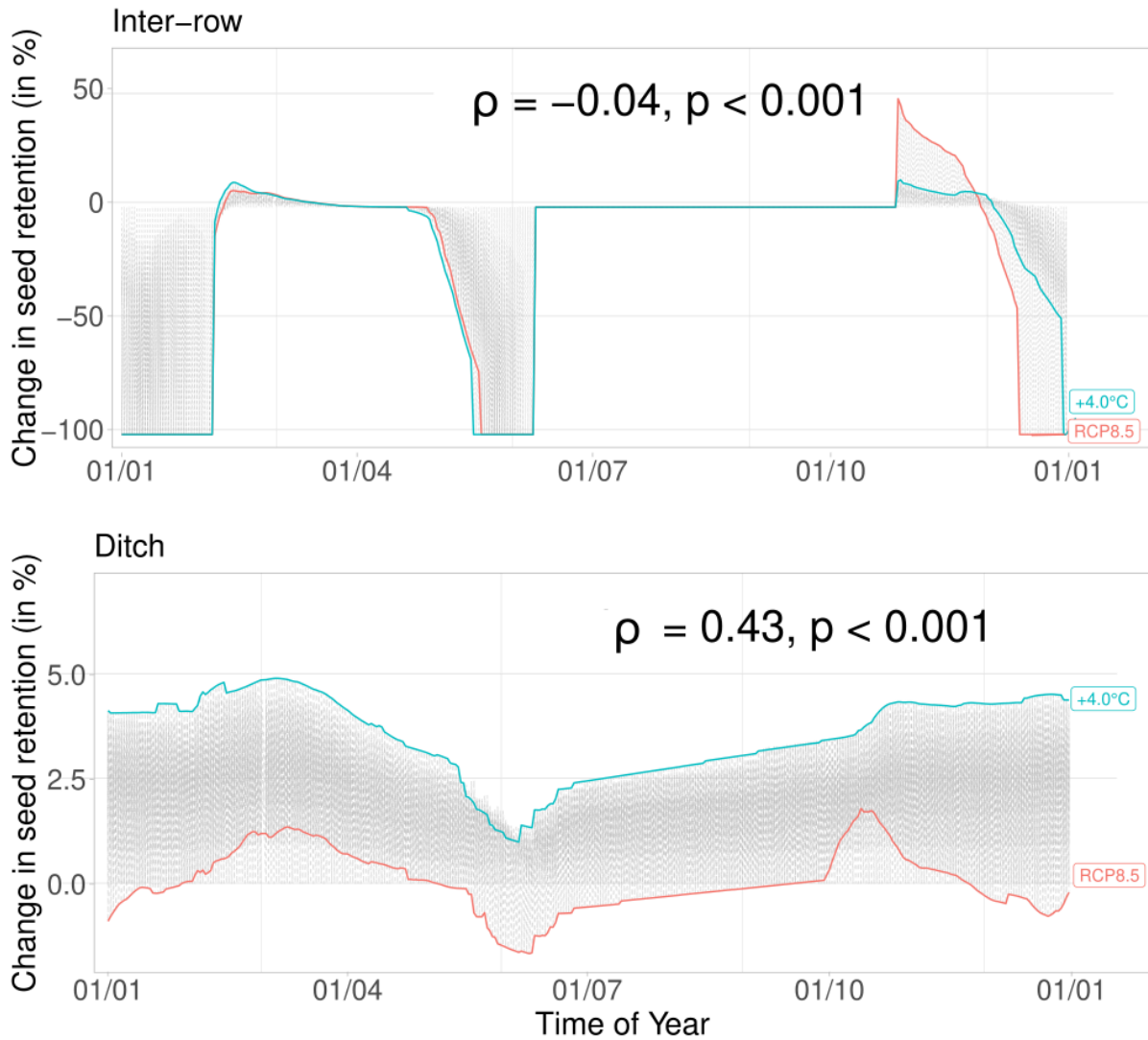


Figure IV. 8. Evolution of the change in seed retention values aggregated over 10 years of simulation relative to the control (i.e. +0°C) scenario. Simulations produced by the +4°C and RCP 8.5 scenarios are highlighted in blue and red respectively. Other simulations are displayed in gray dotted lines.

IV. 4. Discussion

Overall, this work yielded interesting results, both from a modeling and ecohydrological standpoint. MoVeGrowth is one of the first models to simulate a plurispecific vegetation growth in a Mediterranean setting. As the Mediterranean region will be particularly impacted by climate change, the opportunity to simulate a plurispecific vegetation cover inside one of its staple cultures has interesting perspectives of application.

Inside ditches, the water friction decreased as the air temperature rose, with a 5% reduction on average for the two scenarios with the highest rise in air temperature (i.e., +4°C). This result coincides with previous results predicting a reduction in vegetation levels

caused by climate change (Lopez et al., 2021). As the start of the senescence phase is determined by a sum of temperature, it is plausible that higher air temperatures contributed to reaching this phase faster, while also accelerating the senescence itself. Thus, the plant community was overall less developed around the year, which reduced the friction it could generate on water flows. Interestingly, the rise in air temperature coincided with a rise in seed retention, reaching around a 5% increase for the +4°C scenario, whereas the average seed retention under the RCP 8.5 scenario was not different from the control scenario. Considering rainfall is the main difference between the +4°C climate scenario and the RCP 8.5 scenario, this result indicates water stress plays an important role in seed retention.

Inside inter-rows, water friction and seed retention relative change were affected by the rise in air temperature, but the near-zero values of the associated correlation coefficients and the absence of correlation between vegetation cover and climate scenarios entails cautiousness during the interpretation. Especially, the 50% increase in friction between October and January under the RCP 8.5 scenario points towards the possibility to reduce surface runoff and erosion during this period of time as climate change continues. However this tendency is reversed during the winter as friction is predicted to reduce by 100% (i.e., divided by 2). Since this period of time (i.e., October to March) is typically characterized by intense rainfall events in the present time, further investigation to entangle the effects responsible for the mixed results observed is crucial.

For agricultural ditches, the marginal decrease in friction generated by vegetation against water flows implies ditches could potentially host a permanent vegetation with benefits for biodiversity in Mediterranean agrosystems without consequences for their role of runoff collection. Likewise, seed retention is expected to increase by a similar margin than the decrease in water friction under the RCP 8.5 scenario. Thus, seed dispersal by hydrochory is not threatened by climate change according to our results, which is in contradiction with recent observations (Mendes et al., 2024).

Other changes in biotic and abiotic factors due to climate change are likely, but could not have been easily implemented in the present version of the model. For example, vegetation communities are expected to shift towards more drought-resilient species (Pérez-Navarro, et al., 2023; Saatkamp et al., 2023), but selection is limited to the species present in the input table in our model, and neither mutation nor migration are simulated. Drought-resilient species are commonly associated with a reduced leaf area, a lower number of ramifications, and/or a reduced growth rate (Lopez-Iglesias et al., 2014). These traits directly or indirectly contribute to the potential friction generated by vegetation on water

flows (Rudi et al., 2022; 2021), thus differentiating scenarios with different species pools might have produced lower friction values following the air temperature rise across scenarios.

Prior to this model, seed retention had only been simulated empirically (Rudi et al., 2021). With simple assumptions concerning plant architecture, the model is able to provide friction values consistent with experimental results. As traits related with plant architecture can be hard to find in the literature (Kattge et al., 2020), these simplifications offer a satisfying compromise expanding the reusability of the model to different geographical situations than those it was developed for, i.e. in other winegrowing regions, both in France and other winegrowing regions under a Mediterranean climate.

Conclusion

MoVeGrowth is a model resulting from the aggregation of previously established formalisms to obtain a plurispecific vegetation growth model describing vineyard inter-rows and agricultural ditches in a Mediterranean climate. The evaluation procedure showed that MoVeGrowth has a tendency to underestimate vegetation characteristics, especially in the case of inter-rows. As a consequence, future applications of this model should include a new calibration procedure, regardless of the climate in which the inter-row and ditch simulations are located.

Going back to the objective of this study, spatializing the model would primarily allow for taking into account the upstream water flows entering the simulated ditch section, which would allow for observing differences at the watershed scale. At a regional scale, it could help track geographical differences in the interactions between vegetation and water due to climate change. In particular, altitude has been shown to increase the temperature rise linked with climate change in otherwise similar geographical regions (Alikadic et al., 2019, Ohmura, 2012). As our results showed the rise in temperature was the driving factor of change in vegetation dynamics, sites situated along an altitudinal gradient are likely to have different responses to climate change, which requires different adaptation strategies to face the upcoming challenges faced by agrosystems.

Chapitre V. Discussion et conclusion générale

Synthèse des résultats de la thèse

La banque de graines du sol reflète l'intensité des pratiques d'enherbement : en effet, au sein d'une même parcelle viticole la banque de graines du sol était plus diverse dans les inter-rangs enherbés que dans les inter-rangs labourés. Plus généralement, la banque de graines du sol dans les espaces non cultivés (i.e., les inter-rangs de vigne, les tournières, et les fossés agricoles) était plus diverse dans un paysage agricole où les pratiques extensives sont généralisées. Ces résultats sont les premiers acquis pour les parcelles viticoles, et rejoignent des observations obtenues précédemment dans des cultures d'oliviers (Carpio et al., 2022), ainsi que dans des cultures plus éloignées en terme de caractéristiques et de climat (Mahé et al., 2021; Fried et al., 2009). Ces résultats se démarquent également de la majorité de la littérature existante sur le sujet par la prise en compte du mode de dispersion dans la répartition observée de la banque de graines du sol en termes de richesse spécifique et de densité. Cette prise en compte a notamment conduit à observer une part plus importante d'espèces zoochores (i.e., déplacées par les animaux) dans les fossés comparativement à la parcelle, ou encore la prévalence des espèces barochores (i.e., déplacées par la gravité) au sein de la banque de graines du sol des inter-rangs de vigne.

Ensuite, le travail de thèse a montré que l'hydrochorie contribue également à la dispersion des espèces végétales au sein des parcelles agricoles. En particulier, notre expérimentation a montré que l'amplitude de la dispersion dépend des caractéristiques de la parcelle, le couvert végétal et la rugosité impactant négativement le déplacement des graines. Notre expérimentation a aussi mis en évidence l'influence des caractéristiques des graines, les graines les plus lisses et sphériques étant plus susceptibles d'être dispersées par une lame d'eau ruissellée que les graines disposant de crochets ou de poils. Ces observations rejoignent la littérature existante principalement développée par les sciences du sol (ex : Janeau et al., 2022; de Rouw et al., 2018). Ces résultats ouvrent des perspectives nouvelles pour la gestion de l'enherbement dans les milieux viticoles, pour la biodiversification comme pour la lutte contre la dispersion d'espèces invasives.

Enfin, les résultats de la modélisation du couvert végétal selon des scénarios climatiques induisant une augmentation de la température de l'air indiquent une diminution de la friction générée par les interactions végétation-eau. La croissance plus importante

permise par l'augmentation des températures résulte en effet d'une sénescence plus précoce et plus rapide qu'observée actuellement, ce qui conduit à des niveaux de végétation plus bas lors des épisodes pluvieux intenses, et par conséquent une diminution de la friction générée par le couvert. En ce sens, ce résultat rejoint d'autres résultats de simulations ultérieurs prédisant une baisse de la végétation dans le bassin méditerranéen causée par l'augmentation de l'évapotranspiration (He et al., 2022). L'effet de cette baisse de friction aurait des conséquences potentiellement bénéfiques sur la capacité de canalisation du ruissellement des fossés, ainsi que sur la circulation des graines par hydrochorie. Toutefois, la baisse de la friction générée par la végétation présente dans les inter-rangs de vigne signifierait une plus grande vulnérabilité des parcelles viticoles à l'érosion des sols, ainsi qu'un risque accru de concentrations plus élevées en résidus phytosanitaires dans les eaux de ruissellement rejoignant le réseau hydrographique causé par la réduction de leur captation par la litière produite par la végétation (Dagès et al., 2023). Ces enseignements issus de l'exploration numérique ont été rendus possible par le développement de MoVeGrowth, qui figure parmi les premiers modèles écohydrologiques couplant la croissance mécaniste de la végétation et son interaction avec l'eau.

Perspectives

Quel apport de la démarche couplant observation-expérimentation-simulation?

L'approche couplant observation, expérimentation et modélisation a nourri une réflexion permanente sur les attentes liées au travail de thèse. L'observation de la banque de graines du sol a nourri le questionnement concernant la facilité des graines à être déplacées à l'intérieur de la parcelle et en dehors, et a aussi permis une caractérisation de l'état actuel de la végétation au sein des parcelles viticoles et dans leurs fossés attenants sur laquelle s'appuyer lors de la phase de modélisation. L'expérimentation du déplacement des graines par hydrochorie a permis de fournir des hypothèses pour expliquer l'abondance de certaines espèces retrouvées au sein de la banque de graines du sol, en particulier à propos de l'influence d'un couvert végétal au sein d'un inter-rang de vigne sur le déplacement des graines. L'expérimentation a par ailleurs permis l'obtention de valeurs empiriques de ruissellement au sein d'une parcelle viticole, ainsi qu'une meilleure perspective concernant les événements majeurs de pluie qui ont pu être utilisés lors du travail de modélisation. De manière générale, le travail de modélisation a incité à une réflexion permanente sur les traits

nécessaires à la simulation des objets et phénomènes étudiés, ainsi qu'à leur facilité d'obtention.

Apports de l'interdisciplinarité

Dans ce travail de thèse, nous avons souhaité adopter une approche interdisciplinaire, en accord avec la définition institutionnelle d'INRAE "d'interaction et la coopération de plusieurs disciplines de domaines différents autour d'objets et de projets communs.". Dans le cadre du projet de thèse, ce souhait s'est principalement incarné dans un travail mêlant écologie et hydrologie. L'association n'est pas nouvelle (Rudi et al., 2021; Rinaldo et al., 2018; Ludwig et al., 2005), mais la périodicité des flux d'eau parcourant nos lieux d'études démarque ce travail de la littérature existante.

La mise en œuvre de la démarche écohydrologique a pris corps dans l'utilisation du principe de traits fonctionnels développé au sein de la recherche en écologie à des fins de modélisation hydrologique. Les traits fonctionnels sont notamment définis par leur simplicité d'acquisition sur le terrain et leur lien direct avec une fonction (Violle et al., 2007). Comme l'a montré le travail sur l'évolution de la friction générée par la végétation sur l'écoulement de l'eau selon différents scénarios climatiques, cette dualité facilité d'acquisition/mesure d'une fonction peut se retranscrire convenablement dans la modélisation. Ce travail s'est concentré sur une application des traits fonctionnels que sont la hauteur du couvert et sa couverture végétale, cependant d'autres applications sont envisageables. L'augmentation de la surface foliaire, ainsi que de la couverture végétale en général, ont notamment été reliées à la réduction de l'érosion du sol (Garcia et al., 2020; Moreau et al., 2020), ainsi qu'indirectement à la captation de pesticides au sein d'un flux d'eau (Dagès et al., 2023).

Le travail d'expérimentation sur l'hydrochorie lors de ruissellement de surface a impliqué l'utilisation du rapport masse/volume, qui a pu être obtenu grâce à la mesure des traits fonctionnels que sont la masse, la longueur, et la largeur des graines. A ce titre, le rapport masse/volume n'est pas un trait fonctionnel à part entière malgré son influence sur la flottabilité des graines (Carthey et al., 2016).

Caractérisation de la banque de graines du sol par la méthode de germination spontanée

La représentativité et la caractérisation de la banque de graines du sol à travers divers gradients environnementaux et/ou à différentes échelles est un enjeu majeur de la recherche sur le sujet. Cependant, les expérimentations de germination spontanée nécessitent des investissements importants, de la récolte des échantillons à leur mise en place dans des conditions favorables, limitant leur généralisation.

Par ailleurs, la comparaison de la banque de graines du sol avec la végétation observée à la surface est un enjeu important des projets de conservation. En effet, cette comparaison est souvent utilisée pour estimer la fréquence et/ou l'intensité des perturbations sur le site étudié, avec une corrélation positive entre le niveau de perturbation et la similarité entre la banque de graines du sol et la végétation observée en surface (Hopfensperger, 2007).

Toutefois les agroécosystèmes semblent être un cas particulier, certaines études observant le lien positif entre l'intensité des perturbations et la similarité sur toute la parcelle (Andreasen et al., 2018; Shaukat & Siddiqui, 2003; Dessaint et al., 1997), tandis que d'autres l'observent seulement dans les bordures de parcelle (Fried et al., 2009). Une manière de poursuivre le travail effectué sur la banque de graines du sol serait donc de le compléter avec une caractérisation de la végétation observée en surface.

Néanmoins un tel projet pourrait rapidement se heurter à des contraintes temporelles, humaines et financières. Dans ce contexte, l'automatisation d'une partie du processus pourrait permettre la facilitation de la mise en œuvre d'un tel projet.

Les progrès de l'intelligence artificielle dans la reconnaissance des espèces végétales ont notamment conduit au développement de l'application Pl@ntNet (Joly et al., 2016), permettant à une personne équipée d'un smartphone d'obtenir rapidement l'identification d'une plante. L'existence de modèles tels que celui de Pl@ntNet permettent donc l'automatisation de l'identification des espèces végétales observées pouvant être réalisée en même temps que la capture d'image (Champ et al., 2020). L'identification des espèces végétales peut donc s'automatiser dans le cadre de relevés de végétation, cependant la performance des modèles de reconnaissance d'image diminue dans le cadre d'individus à des stades de développement précoces.

En parallèle à l'identification des plantules et à la maintenance du dispositif expérimental, une prise de vue des 286 échantillons utilisés a été effectuée. Les images récoltées ont permis une correction a posteriori de certaines identifications d'espèces, mais

pourraient également représenter une opportunité précieuse d'améliorer la reconnaissance précoce d'espèces végétales par imagerie. L'annotation du jeu de données, l'entraînement d'un modèle d'apprentissage supervisé et la comparaison de ses performances à celles du modèle utilisé par l'application Pl@ntNet fera l'objet d'un futur projet de recherche. Ce travail pourrait donc contribuer à faciliter la réalisation d'une expérimentation de germination spontanée en permettant l'identification automatisée des plantules ayant émergé des échantillons collectés.

Expérimentation sur l'hydrochorie lors de ruissellement de surface dans les inter-rangs de vigne

En résumé, les écueils de l'expérimentation découlent de la difficulté d'étudier les processus écohydrologiques de manière à satisfaire les attentes de l'écologie et de l'hydrologie. En écho avec le positionnement scientifique exposé dans le premier chapitre, la pertinence des résultats du point de vue de l'écologie a été favorisée face à l'hydrologie. Concrètement, cela s'est traduit par le choix de réaliser l'expérimentation en conditions naturelles, avec la pluviométrie existante, plutôt que de recourir à l'utilisation de simulateurs de pluie courante dans ce type d'expérience (Janeau et al., 2022 ; Grellier et al., 2012, 2013 ; Aerts et al., 2006). Ce choix a eu deux conséquences : l'absence de répétition de l'expérience causée par une pluviométrie anormalement basse pour la période (rapport 2023 de Météo France), et la nécessité d'installer un dispositif expérimental permettant de mesurer le ruissellement. Le dispositif expérimental en lui-même a fonctionné comme il le devait, mais son envergure représentait une gêne pour les techniciens du domaine viticole qui a entraîné son retrait quand sa présence est devenue problématique. Une méthode alternative reposant davantage sur le continuum observation-expérimentation-modélisation pourrait permettre d'alléger ce dispositif, en couplant une modélisation mécaniste et des mesures de propriétés du sol sur la zone d'étude pour simuler la lame d'eau ruisselée (Pijl et al., 2023).

Modélisation

Domaine d'applicabilité du modèle

Le modèle MoVeGrowth a uniquement été utilisé dans un contexte méditerranéen au cours du projet de thèse, cependant il n'existe pas de limitation intrinsèque au modèle à son application à d'autres contextes climatiques. Néanmoins, les simplifications réalisées

concernant les écoulements au sein des inter-rangs et des fossés nécessiteraient une adaptation à des climats plus tempérés.

L'implémentation d'une modélisation mécaniste des écoulements d'eau serait par ailleurs une piste de développement futur du modèle, au coût de l'augmentation de la complexité et du temps de calcul du modèle. De fait, une version allégée du modèle a été utilisée dans le cadre d'un projet de modélisation intégrée du devenir des pesticides dans un paysage viticole méditerranéen (méta-modèle MIPP, Dagès et al., 2024). Ce méta-modèle comprend une modélisation mécaniste du ruissellement plus précise que la méthode du *curve number* utilisée dans MoVeGrowth, au coût d'un temps de simulation supérieur de plusieurs ordres de grandeur (i.e., une simulation de 10 ans dure 10 secondes avec MoVeGrowth, plus d'une semaine pour le métamodèle). Le travail d'incorporation du modèle de croissance végétale au sein du méta-modèle MIPP a consisté à adapter son fonctionnement à la plateforme de modélisation paysagère OpenFLUID (Fabre et al., 2010), ce qui représente une première étape pour une spatialisation éventuelle de MoVeGrowth.

Traits des plantes

En écho à la simplification effectuée sur la modélisation des écoulements d'eau, l'architecture des plantes a été résumée par leur surface foliaire et la surface de sol recouverte à maturité, en faisant l'hypothèse que la plante s'inscrivait dans un trapèze régulier. Même si cette simplification assez forte a produit des résultats convaincants, une meilleure prise en compte des différences d'architecture entre les espèces végétales simulées pourrait être envisagée. Si cette prise en compte n'augmentera pas la complexité du modèle en lui-même, elle pourrait toutefois diminuer son applicabilité. En effet, bien que cette meilleure prise en compte de l'architecture des plantes puisse reposer sur des traits fonctionnels faciles à acquérir (diamètre de la tige, largeur de la corolle, rapport extrémité basale/extrémité apicale, ...), l'existence de telles valeurs dans les bases de données conséquentes telles que TRY s'est révélée plus rare qu'attendue (Kattge et al., 2022). Les milieux arides et semi-arides sont en effet moins représentés dans les bases de données que les biomes tempérés (Maitner et al., 2023; Thomas et al., 2020).

Modélisation mécaniste

Le choix de faire de MoVeGrowth un modèle mécaniste et déterministe s'inscrit dans l'objectif de produire un outil compréhensible, modifiable et utilisable par le plus grand nombre. Face aux contraintes des expérimentations *in situ*, la modélisation permet l'exploration de nombreux scénarios, qui peuvent permettre d'anticiper des conditions futures, d'étudier les trajectoires que pourrait suivre un milieu à partir de sa situation présente, voire même de se détacher du réalisme pour isoler l'effet d'un paramètre en particulier, comme nous l'avons fait en augmentant seulement la température de l'air. Par ailleurs, les choix de modélisation faits pour faciliter la compréhension du fonctionnement du modèle permettent de maintenir un temps de simulation bas. L'accessibilité et le réemploi du modèle sont toutefois limités par la disponibilité des données relatives aux espèces, et ce malgré les simplifications apportées à la prise en compte des variations interspécifiques des traits utilisés.

Cependant il pourrait être envisageable d'utiliser MoVeGrowth en simulant des espèces types représentatives d'une stratégie écologique en particulier, par exemple la CSR de Grimes (Grime et Pierce, 2012), les stratégies r et K (MacArthur et Wilson, 2001), ou encore la classification de Julve (Julve, 1998). La stratégie CSR répartissant les espèces selon que leurs traits favorisent la **Compétition**, la tolérance aux **Stress** abiotiques, ou leur caractère **Rudéral** (i.e., la tolérance aux pratiques agricoles) serait particulièrement intéressante à appliquer à notre cas d'étude car les stratégies sont fortement corrélées à trois indicateurs associés à l'appareil végétatif : la surface foliaire absolue, la surface foliaire relative à la masse, et le rapport masse sèche foliaire sur masse sèche totale (Pierce et al., 2017). Par conséquent, la modélisation d'un couvert végétal composé d'espèces représentant une ou plusieurs stratégies permettrait de capturer finement l'effet de l'évolution de la composition des communautés végétales sur la friction générée sur les écoulements d'eau.

Par ailleurs, la modélisation du ruissellement pourrait être modifiée en faveur de formalismes plus adaptés aux écoulements en lame mince. En effet, la précision de la relation utilisée pour le calcul du coefficient de Manning-Strickler diminue drastiquement en dessous d'un seuil de hauteur de lame d'eau (Hou et al., 2018). Indépendamment du changement de formalisme, le pas de temps journalier du modèle correspond mal aux besoins et à la temporalité de ce type d'écoulement. Ces deux modifications représentent une source potentielle d'augmentation du temps de calcul nécessaire au modèle, menaçant la volonté d'une simulation accessible mentionnée précédemment. Cette augmentation pourrait

cependant être réduite au strict nécessaire, notamment par le développement d'un pas de temps variable consistant à réduire le pas de temps uniquement lorsque l'écoulement d'eau doit être simulé (Leandro et al., 2014).

Contribution de l'hydrochorie dans la dispersion de la biodiversité

Nous avons fait le choix de nous concentrer sur la dispersion secondaire par hydrochorie, cependant d'autres modes de dispersion existent. Ce choix s'appuyait sur la prévalence de l'hydrochorie par rapport aux autres modes de dispersion observée lors des événements de dispersion secondaire (der Weduwen et Ruxton, 2019; Nilsson et al., 2010; Hampe, 2004). Il s'appuyait aussi sur l'importance des événements de ruissellement au sein des inter-rangs de vigne et des fossés agricoles, avec le souhait de transposer la littérature existante sur l'hydrochorie dans les cours d'eau permanents à des éléments linéaires ponctuellement submergés. Toutefois la littérature sur la dispersion des graines dans les agroécosystèmes (Petit et al., 2011; Benvenuti, 2007) - ainsi que nos observations empiriques lors de déplacements sur les parcelles - nous amène à questionner la part relative de chaque mode de dispersion dans la circulation de la biodiversité des agroécosystèmes méditerranéens.

Malgré les difficultés rencontrées mentionnées précédemment, l'hydrochorie semble le mode de dispersion le plus simple à suivre car à sens unique et la surface où rechercher les graines est relativement restreinte par les limites imposées par ce qui contraint l'écoulement de l'eau (i.e., les berges, les rangs de vigne, l'inclinaison de la pente). En comparaison, l'anémochorie (dispersion par le vent) et la zoochorie (dispersion par les animaux) peuvent théoriquement disperser les graines jusqu'à n'importe quel point dans une zone géographique donnée. Par conséquent, les études empiriques sur l'anémochorie et la zoochorie s'appuient sur la capture des graines ou de leur vecteur, ce qui rend difficile l'estimation exacte des capacités de dispersion puisque l'événement de dispersion est interrompu (Lemke et al., 2009).

Comme pour l'hydrochorie, les modèles mécanistes simulant l'anémochorie et la zoochorie s'appuient sur la modélisation de leur vecteur, avec des conséquences identiques sur leur complexité ainsi que sur la difficulté de conclure quant à la probabilité d'implantation réussie des graines simulées (Nathan et al., 2002). Des modèles d'écologie théorique existent également, certains basés sur le concept de *pattern oriented modelling*, qui repose sur le développement d'un modèle axé sur la reproduction d'un schéma observé (Grimm et al., 1996). La finalité de ces approches est de faire émerger des comportements à

partir d'axiomes simples concernant la reproduction, le développement, et la dispersion des êtres vivants. Un travail préliminaire dans un paysage agricole méditerranéen typique a été réalisé en marge du projet de thèse, en simulant le déplacement de graines anémochores, zoochores et hydrochores selon des règles de déplacement simples associées à des probabilités de dispersion suivant des distributions gaussiennes (mémoire de Q. Guilloit, 2023).

Connaissances utiles aux acteurs

Ce travail de thèse a permis d'acquérir des connaissances pouvant justifier plusieurs recommandations aux agriculteurs et aux acteurs du monde agricole. Tout d'abord, l'étude de la banque de graines du sol doit permettre d'encourager le développement préférentiel d'un couvert végétal spontané par rapport à l'ensemencement de mélanges spécialisés (par ex., plantes nitrophiles, plantes mellifères, ...). En effet des espèces végétales pouvant fournir les services écosystémiques visés par les semences commerciales ont été observées dans la banque de graines du sol étudiée lors du projet de thèse.

En plus des avantages économiques (pas de dépenses en semences, charge de travail liée au désherbage réduite, ...), privilégier la végétation issue de la banque de graines du sol permet d'éviter les risques d'introduction d'espèces végétales exogènes pouvant avoir des conséquences indésirables, ou plus simplement d'assurer l'auto-régénération de la couverture végétale.

L'expérimentation sur l'hydrochorie lors d'un épisode de ruissellement de surface offre des perspectives intéressantes pour les écologues notamment. Elle a permis de réaffirmer le besoin de protéger les sols agricoles de l'érosion grâce à une couverture végétale suffisamment fournie. De plus, le remaniement de la surface du sol dans les inter-rangs de vigne pourrait être un moyen d'accélérer leur revégétalisation en créant des espaces propices à leur dépôt et leur germination.

Enfin, le travail de modélisation pourrait être utilisé comme un outil d'aide à la décision pour appuyer les stratégies d'adaptation des paysages agricoles au changement climatique. Permettre aux collectivités d'anticiper les conséquences d'une baisse ou d'une hausse du niveau de végétation dans les linéaires agricoles revêt en effet une importance capitale au vu des enjeux de santé publique, prévention des risques, et de politique publique.

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Liste des publications

- Publication acceptée

Faucher, M., Grellier, S., Chaudron, C., Janeau, J. L., Rudi, G., & Vinatier, F. (2024). Mediterranean vineyard soil seed bank characterization along a slope/disturbance gradient: Opportunities for land sharing. *Agriculture, Ecosystems & Environment*, 361, 108821. <https://doi.org/10.1016/j.agee.2023.108821>

- Publications soumises ou à soumettre

Faucher, M., Grellier, S., Chaudron, C., Janeau, J. L., Rudi, G., & Vinatier, F., Secondary seed dispersal by hydrochory during surface runoff inside a Mediterranean vineyard, soumis à *Ecohydrology*

Faucher, M., Dagès, C., Garcia, L., Metay, A., Thöni, A., Voltz, M., & Vinatier, F., MoVeGrowth, an ecohydrological model developed to simulate plant-water friction in inter-rows and agricultural ditches in Mediterranean vineyards, en préparation pour soumission à *Ecological Modelling*

- Communications internationales:

Faucher M., Vinatier F., Bailly J.-S. (2022-11-21). Hydrochory as a means for Mediterranean vineyards revegetation. Presented at SFE² GfÖ EEF - Joint meeting, International Conference on Ecological Sciences, Metz, France (2022-11-21), <https://hal.inrae.fr/hal-03874472>

Faucher M., Vinatier F., Bailly J.-S. (2022-05-23). Using hydrochory for agricultural landscape revegetation. Presented at European Geosciences Union 2022, Vienne, Autriche (2022-05-23 - 2022-05-28), <https://hal.inrae.fr/hal-03737975>

Annexes

Annexe A. Analyses physico-chimiques

Field	Interrow	Transect	PH	CARBON		SOM	N		PHOSPHATE	MAGNESIU	MgO	POTASSIU	K2O	SODIU	Na2O	CEC
				E (g/kg)	(g/kg)	(g/kg)	C/N	M		(mg/kg)	M	(mg/kg)	M	(mg/kg)		
P1	1	T1	8.3	11.6	19.95	1.3	8.92	155	7.7	155.16	3.72	175.21	0.66	20.46	81	
P1	1	T2	8.5	9	15.48	0.69	13.04	93	6.53	131.58	2.77	130.47	0.37	11.47	73	
P1	1	T3	8.2	17.4	29.93	1.31	13.28	163	11.64	234.55	9.73	458.28	1.31	40.61	125	
P1	1	T4	8.6	11.3	19.44	0.92	12.28	131	9.15	184.37	5.79	272.71	0.45	13.95	91	
P1	1	T5	8.3	15.3	26.32	1.29	11.86	114	10.84	218.43	6.29	296.26	0.89	27.59	107	
P1	1	T6	8.3	17.7	30.44	1.54	11.49	136	11	221.65	6.21	292.49	0.53	16.43	109	
P1	3	T1	8.5	10.2	17.54	0.82	12.44	89	09.09	183.16	3.16	148.84	0.5	15.5	99	
P1	3	T2	8.5	10.2	17.54	0.8	12.75	85	7.58	152.74	4.23	199.23	0.6	18.6	98	
P1	3	T3	8.6	9.3	16	0.9	10.33	84	7.25	146.09	3	141.3	0.5	15.5	86	
P1	3	T4	8.5	15.5	26.66	1.4	11.07	276	10.09	203.31	7.15	336.77	0.94	29.14	99	
P1	3	T5	8.5	16	27.52	1.38	11.59	104	12.19	245.63	5.9	277.89	0.72	22.32	109	
P1	3	T6	8.3	17.3	29.76	1.64	10.55	111	10.91	219.84	5.3	249.63	0.6	18.6	111	

P1	5	T1	8.1	25.3	43.52	2.26	11.19	221	10.7	215.61	5.88	276.95	0.86	26.66	145
P1	5	T2	8.5	12.1	20.81	01.01	11.98	95	10.23	206.13	3.33	156.84	0.78	24.18	112
P1	5	T3	8.5	11	18.92	0.81	13.58	91	7.31	147.3	03.03	142.71	0.54	16.74	84
P1	5	T4	8.3	9.6	16.51	0.91	10.55	92	6.74	135.81	04.01	188.87	0.39	12.09	77
P1	5	T5	8.1	17.8	30.62	1.37	12.99	100	9.15	184.37	11.35	534.59	0.7	21.7	108
P1	5	T6	8.5	8.8	15.14	01.03	8.54	98	7.19	144.88	4.15	195.47	01.05	32.55	88
P2	1	T1	8.3	22.9	39.39	1.89	12.12	127	11.19	225.48	4.51	212.42	0.62	19.22	129
P2	1	T2	8.6	17.3	29.76	1.2	14.42	192	10.43	210.16	5.54	260.93	0.73	22.63	107
P2	1	T3	8.6	11.7	20.12	0.73	16.03	59	14.7	296.21	4.21	198.29	1	31	209
P2	1	T4	8.5	12.1	20.81	1	12.1	123	9.77	196.87	05.06	238.33	0.67	20.77	126
P2	1	T5	8.3	19.3	33.2	1.5	12.87	247	12.64	254.7	9.58	451.22	0.48	14.88	136
P2	1	T6	8.1	27.5	47.3	2.35	11.7	311	13.8	278.07	12.59	592.99	0.92	28.52	148
P2	1	T7	8.3	22.7	39.04	1.58	14.37	208	11.2	225.68	7.61	358.43	0.63	19.53	132
P2	3	T1	8.2	29.2	50.22	1.97	14.82	196	11.4	229.71	8.58	404.12	0.82	25.42	151
P2	3	T2	8.5	17.6	30.27	1.38	12.75	206	12.16	245.02	7.67	361.26	0.6	18.6	120
P2	3	T3	8.4	19.3	33.2	1.45	13.31	188	13.15	264.97	10.02	471.94	0.69	21.39	113
P2	3	T4	8.2	19.1	32.85	1.42	13.45	280	12.1	243.82	7.87	370.68	0.63	19.53	129

P2	3	T5	8	24.1	41.45	1.98	12.17	264	13.67	275.45	11.18	526.58	0.66	20.46	126
P2	3	T6	8.3	26.9	46.27	1.61	16.71	235	14.38	289.76	12.58	592.52	01.09	33.79	131
P2	5	T1	8.5	14.9	25.63	0.99	15.05	147	10.48	211.17	6.77	318.87	0.51	15.81	106
P2	5	T2	8.5	14.1	24.25	0.92	15.33	77	11.2	225.68	6.96	327.82	0.75	23.25	138
P2	5	T3	8.5	9.8	16.86	0.73	13.42	62	10.05	202.51	5.37	252.93	0.7	21.7	142
P2	5	T4	8.4	15	25.8	0.98	15.31	163	11.05	222.66	7.6	357.96	0.67	20.77	128
P2	5	T5	8.2	20.4	35.09	1.59	12.83	253	11.93	240.39	10.76	506.8	0.7	21.7	129
P2	5	T6	8.4	15.2	26.14	1.14	13.33	94	8.46	170.47	4.96	233.62	0.63	19.53	112
P2	5	T7	8.2	26.8	46.1	2.23	12.02	180	11.49	231.52	7.41	349.01	0.83	25.73	164
P2	2	T1	8.6	9.9	17.03	0.76	13.03	63	8.54	172.08	3.27	154.02	0.67	20.77	83
P2	2	T2	8.5	10.3	17.72	0.86	11.98	60	10.74	216.41	4.85	228.44	0.77	23.87	159
P2	2	T3	8.5	13.6	23.39	1.1	12.36	110	9.83	198.07	6.73	316.98	0.55	17.05	126
P2	2	T4	8.3	18.9	32.51	1.4	13.5	233	9.67	194.85	9.68	455.93	0.56	17.36	121
P2	2	T5	8	24.6	42.31	1.91	12.88	187	10.87	219.03	08.04	378.68	0.82	25.42	128
P2	2	T6	8.4	14.3	24.6	01.02	14.02	124	8.59	173.09	5.66	266.59	0.41	12.71	100
P2	2	T7	8.2	19.4	33.37	1.62	11.98	179	10.35	208.55	07.02	330.64	0.57	17.67	125
P2	4	T1	8.5	14	24.08	01.02	13.73	127	9.29	187.19	3.47	163.44	1	31	87

P2	4	T2	8.5	11.2	19.26	0.85	13.18	32	6.82	137.42	3.13	147.42	0.95	29.45	138
P2	4	T3	8.5	12	20.64	01.08	11.11	111	9.26	186.59	7	329.7	0.89	27.59	105
P2	4	T4	8.3	16	27.52	1.44	11.11	148	10.52	211.98	12.08	568.97	0.65	20.15	94
P2	4	T5	8.1	20	34.4	1.67	11.98	183	11.86	238.98	9.65	454.52	0.77	23.87	131
P2	4	T6	8.3	20.4	35.09	1.44	14.17	131	10.22	205.93	6.43	302.85	1	31	117
P2	4	T7	8.4	18.7	32.16	1.46	12.81	128	9.29	187.19	6.61	311.33	0.46	14.26	130
P2	6	T1	8.5	14.9	25.63	1.23	12.11	130	10.24	206.34	5.89	277.42	0.79	24.49	111
P2	6	T2	8.5	12	20.64	0.95	12.63	61	10.75	216.61	8.48	399.41	0.68	21.08	131
P2	6	T3	8.6	8.6	14.79	0.87	9.89	70	8.62	173.69	6.55	308.51	0.6	18.6	133
P2	6	T4	8.4	14.4	24.77	01.03	13.98	111	11.36	228.9	11	518.1	0.54	16.74	125
P2	6	T5	8.3	17.4	29.93	1.35	12.89	178	11.71	235.96	10.97	516.69	0.59	18.29	140
P2	6	T6	8.1	25.6	44.03	2.25	11.38	163	12.16	245.02	7.71	363.14	1.27	39.37	149
P2	6	T7	8.5	16	27.52	01.06	15.09	144	9.58	193.04	4.65	219.02	0.53	16.43	96

Annexe B. Mean E/S ratio (number of seedlings counted divided by the surface of one sample) values and standard deviation for each study site

(P1 : Roujan study site, P2 : Combaillaux study site) and each dispersal mode considered, separated by the zones accounted for in the statistical analyses. Combined effect of dispersal mode and zone sampled was tested by performing an ANOVA on a generalized linear model for each site separately, and differences between zones and between dispersal modes were tested using Tukey tests. Significant differences between dispersal modes are represented by different lowercase letters, and differences between zones are represented by different uppercase letters.

	Anemochory		Barochory		Hydrochory		Zoochory	
	P1	P2	P1	P2	P1	P2	P1	P2
Study site	34.6 +/- 23.1 ^a	32.5 +/- 32 ^a	128 +/- 258 ^b	133 +/- 218 ^c	34 +/- 42.5 ^a	87.3 +/- 102 ^b	28.9 +/- 28.4 ^a	37.2 +/- 34.5 ^a
Field	22.0 +/- 12.84 ^A	20.96 +/- 17.24 ^{Ab}	43.95 +/- 33.64 ^A	160.04 +/- 282.66 ^{Aa}	24.53 +/- 14.04	115.79 +/- 123.27 ^{Aa}	23.6 +/- 18.2	26.56 +/- 29.22 ^{Ab}
Field edge	38.95 +/- 28.14 ^{Bac}	28.93 +/- 24.44 ^{Ba}	248.64 +/- 445.41 ^{Bb}	122.72 +/- 135.7 ^{Bb}	51.78 +/- 78.51 ^a	49.47 +/- 60.88 ^{Aa}	39.76 +/- 44.81 ^a	38.02 +/- 29.8 ^{Ba}
Ditch	47.71 +/- 20.93 ^{Ca}	77.5 +/- 43.88 ^C	150.69 +/- 166.67 ^{Bb}	61.53 +/- 44.28 ^{AB}	33.23 +/- 13.85 ^a	75.36 +/- 43.86 ^B	28.77 +/- 20.97 ^a	74.47 +/- 40.12 ^C

Annexe C. Résultats de l'expérience préliminaire sur la flottabilité des graines marquées et tests statistiques complets réalisés dans le cadre de l'expérimentation

Table C1. Summary of the generalized linear model constructed to test the effect of seed marking and time on the number of floating seeds counted

Factor	F	p-value
Time	2153.29	<0.001
Seed marking	0.16	0.85

Table C2. Factors determining each section permeability to seed proportion of undiscovered seeds (PS). P-values of Kruskal-Wallis tests for each pairwise comparison are given, with Bonferroni correction to account for multiple comparisons, with PS as the dependent variable. Interpretation of significant results is provided.

Explanatory variable	Classes compared	p-value	Interpretation
FVC	low / medium	< 0.001	PS is lower for medium FVC values
	low / high	< 0.001	PS is lower for high FVC values
	medium / high	< 0.001	PS is lower for high FVC values
SL	low / medium	1	
	low / high	1	
	medium / high	1	
SR	low / medium	0.08	
	low / high	<0.001	PS is lower for high SR values
	medium / high	<0.001	PS is lower for high SR values

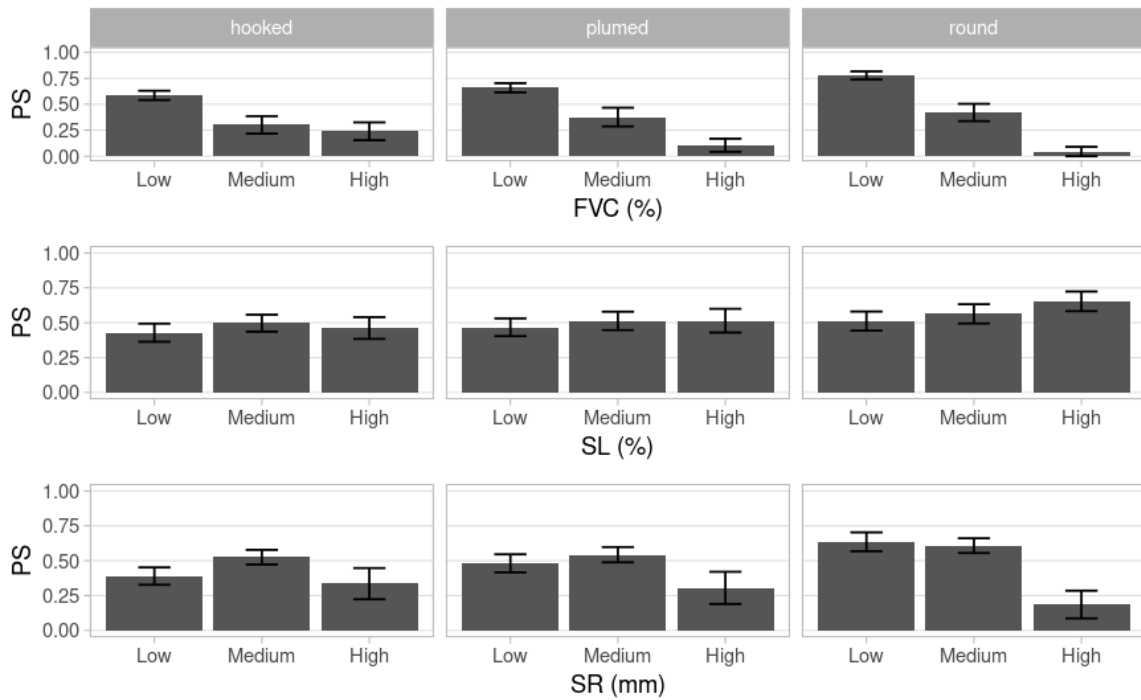


Figure C1. Section permeability to seeds (PS) in relation to each class used to test the effect between PS and fractional vegetation cover (FVC), mean slope in the section (SL), and mean surface roughness (SR), for each seed morphology separately. Error bars indicate the standard errors associated with the mean PS values.

Table C3. Results of the Kruskal-Wallis comparison between PS and fractional vegetation cover (FVC), mean slope in the section (SL), and mean surface roughness (SR), for each seed morphology separately.

Round seeds

	Classes compared	p-value	Interpretation
FVC	low / medium	< 0.001	PS is lower for medium values
	low / high	< 0.001	PS is lower for high values
	medium / high	< 0.001	PS is lower for high values
SL	low / medium	1	
	low / high	0.82	
	medium / high	0.92	
SR	low / medium	1	

	low / high	<0.01	PS is lower for high values
	medium / high	<0.01	PS is lower for high values

Plumed seeds

	Classes compared	p-value	Interpretation
FVC	low / medium	< 0.05	PS is lower for medium values
	low / high	< 0.001	PS is lower for high values
	medium / high	0.06	
SL	low / medium	1	
	low / high	1	
	medium / high	1	
SR	low / medium	0.41	
	low / high	0.63	
	medium / high	0.24	

Hooked seeds

	Classes compared	p-value	Interpretation
FVC	low / medium	< 0.05	PS is lower for medium values
	low / high	< 0.01	PS is lower for high values
	medium / high	1	
SL	low / medium	1	
	low / high	1	
	medium / high	1	
SR	low / medium	0.16	
	low / high	1	
	medium / high	0.43	

Annexe D. Résultats de la comparaison du bilan hydrique de MoVeGrowth avec le modèle WaLIS

The comparison was performed on two references datasets provided with the public version of the WaLIS model, the first one describing a bare soil surface inside an inter-row, and the second one simulating a monospecific herbaceous cover.

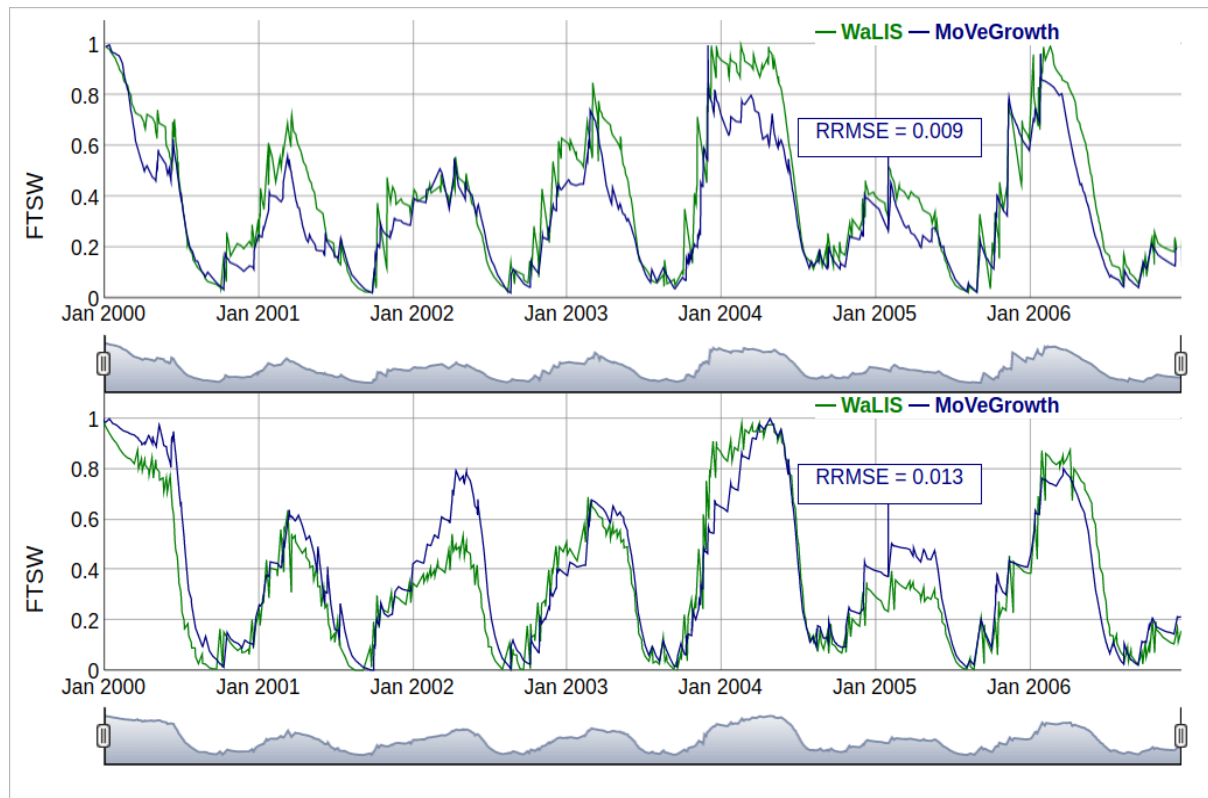


Figure D1. Comparison between transpirable soil water simulated by WaLIS (in blue) and by MoVeGrowth (in green), for two scenarios of vine/interrow computation. The scenarios correspond to the data used to validate WaLIS in Celette et al. (2010) for vineyards in the South of France.

Annexe E. Espèces incluses dans les simulations du modèle MoVeGrowth

Table E1. Species used for the simulations. Species were chosen based on their occurrence among the vegetation surveys which provided the datasets used for the calibration and the evaluation of MoVeGrowth

Inter-row simulations	Ditch simulations
Picris sp.	Lythrum hyssopifolia
Diplotaxis erucoïdes	Elytrigia repens
Convolvulus arvensis	Avena sterilis
Crepis sp.	Torilis arvensis
Cirsium arvense	Galium verum
Sonchus oleraceus	Plantago lanceolata
Amaranthus retroflexus	Picris echioides
Veronica sp.	Erodium malacoides
Geranium rotundifolium	Mercurialis annua
Calendula arvensis	Mentha suaveolens
Portulaca oleracea	Veronica persica
Erodium cicutarium	Euphorbia helioscopia
	Valerianella locusta
	Vicia sativa
	Veronica anagallis aquatica

Annexe F. Fonctions incluses dans le modèle MoVeGrowth

- 1. Vegetation

From the seed stock input at the start of the simulation (arbitrarily set to 10000 for each species), the number of seeds of a species that could break from dormancy is assumed equal to the inverse of the area covered by one individual (*groundcover*, in m²). Values for *groundcover* are taken from the literature and vary from 0.001 to 0.01 m² (Kattge et al., 2022).

If conditions are met, dormancy can be broken for the number of potential seeds previously calculated. The end of dormancy depends on the flowering period of the species (spring, fall, or both). Species flowering in spring/early summer can break dormancy between the 1st of February and the 1st of June, while species flowering during the fall/winter can break dormancy between the 1st of October and the 1st of February. Flowering periods are defined by the 1st day of spring (set to the 1st of February), the 1st day of summer (set to the 1st of June), and the 1st day of fall (set to the 1st of October). For fall species, dormancy break also depends on accumulated rainfall. Dormancy break can be blocked for a fixed number of days by applying a pre-emergence herbicide treatment to the field.

Then, based on the number of non-dormant seeds, the number of seeds that will actually germinate is defined using the hydrothermal time concept developed by Gummerson (1986), which takes into account the cumulative water potential of the soil in addition to the cumulative temperature to determine the duration of germination. The hydrothermal time *HT* is therefore the sum of the respective differences between the daily soil temperature T_{soil} , the observed water potential ψ_{soil} , and their minimum threshold values T_{min} and ψ_{min} (Eq. 1). The hydrothermal time and the base temperature thresholds can be considered constant (45 °C.mPa-1 and 2°C, respectively) for the same species over time, while the minimum water potential can be drawn into among the seeds follows a Gaussian distribution, with ψ_{min50} as mean, and $\sigma(\psi_{min50})$ its standard deviation (Meyer et al., 2000). Values for ψ_{min50} , and $\sigma(\psi_{min50})$ are found in the literature (Köchy & Tielborger, 2007).

$$HT = \sum[(\psi_{soil} - \psi_{min}) * (T_{soil} - T_{min})] \text{ (Eq. 1)}$$

These assumptions lead to the following equation (Bradford, 1990), with *gt* the proportion of germinated seeds, the probit being the inverse of a Gaussian cumulative function, and *d* the number of days since the simulation start, d_{julian} the number of days since 01/01, and d_{germ} the value of d_{julian} when the cohort germinated (Equation no. 2).

$$probit(gt) = \frac{\frac{\sum_{d_{germ}}^d \psi_{soil}^d - \psi_{min50}}{d_{julian} - d_{germ}} * \frac{HT}{\sum_{d_{germ}}^d T_{soil}^d - T_{min}}}{\sigma(\psi_{min})} \quad (\text{Eq. 2})$$

Vegetation growth is based on an equation presented in Duru et al. (2009) for an herbaceous plant cover. The daily growth $GLAI$ (in $m^2 \cdot m^{-2}$) is computed using pre-existing leaf dry mass DW_{leaf} (in $g \cdot g^{-1}$), daily mean temperature T (in $^{\circ}C$), an index of water stress named WI , and a specific daily growth rate LAI_{rate} . A coefficient of soil nitrogen availability NNI is also included, it will be constant during all simulations, and set at 0.3, the value provided for the use of WaLIS in Mediterranean soils (Eq. 3, Celette et al. 2010). The value of LAI_{rate} was first estimated using information about species traits available in the literature. The estimation of the LAI_{rate} led to scaling important differences with experimental data in the first simulation runs, thus a coefficient was added to adjust the growth rate equally over every species, and will be calibrated using experimental data. The value of WI corresponds to the ratio between the simulated transpiration value and the threshold transpiration value under which water stress begins, with values ranging from 0 when the water stress is highest, to 1 when the water is not the limiting factor to vegetation growth.

$$GLAI_j^i(t) = LAI_{rate}^i * DW_{leaf_j}^i(t - 1) * 1,71 \cdot 10^{-3} * T(t)^2 * WI^i(t) * NNI$$

i the species, j the cohort rank (Eq. 3)

In addition to the computation of the daily growth of the vegetation, the model also computes the succession of development stages for each cohort. There are 3 stages, set as vegetative stage, flowering stage, and decaying stage. The succession of stages is controlled by a sum of temperatures STT with threshold values set for every species at every stage. The values were set depending on the flowering season for each species. When a cohort reaches the last stage, its $GLAI$ value is automatically set to 0 and the senescence starts.

Leaf senescence is triggered by reaching a fixed sum of temperatures (LIS , in $^{\circ}C \cdot days$), and is calculated based on the leaf area index at the time of computation, the sum of temperatures since the germination of the cohort (STT , in $^{\circ}C \cdot days$), and the threshold value of sum of temperatures marking the beginning of the senescence stage LIS (Eq. 4). This computation is similar to previous models (Schaphoff et al., 2018), and is associated with a dimensionless parameter k_s governing the slope of the relationship. k_s will be calibrated following the protocol described further in this article.

$$SLAI(t)_j^i = LAI(t - 1)_j^i * \frac{k_s}{\frac{STT_j^i}{LLS^i}} \quad (\text{Eq.4})$$

Based on the *GLAI* and *SLAI*, and the LAI from the day prior, the model then computes the LAI for the current day, for each cohort of each species (Eq. 5).

$$LAI_j^i(t) = LAI_j^i(t - 1) + GLAI_j^i(t) - SLAI_j^i(t) \quad (\text{Eq. 5})$$

Then, the LAI values from each cohort of each species are aggregated into one total leaf area value LA_{TOT} used as an indicator for the whole vegetation cover. The LAI values are weighted by the number of individuals from each cohort, and the surface occupied by one individual from that species according to the literature (in m²) (Eq. 6).

$$LA_{TOT}(t) = \sum_1^i \sum_1^j LAI_j^i(t) * n(plants)_j^i * surface\ of\ 1\ plant^i \quad (\text{Eq. 6})$$

Dry weight partitioning evolves during the development of the vegetation, in order to reflect the shift in resources allocation as the cohort ages. The leaf dry weight DW_{leaf} (in kg.m-2) is calculated as the ratio between the cohort LAI and the leaf area ratio *LAR*, the conversion coefficient between leaf area and global plant mass (in m2.kg-1, Eq. 7).

$$DW_{leaf}_j^i(t) = LAI_j^i(t) / LAR^i \quad (\text{Eq. 7})$$

LAR is a trait measured in the literature, for each species included in the model the TRY database (Kattge et al., 2022) was queried, and the closest value based on APG-III phylogenetic classification was used in the model (Angiosperm Phylogeny Group, 2009). During the first two development stages, DW_{leaf} is used to compute the total dry weight of green tissues in the cohort ($DW_{greenstem}$, in kg.m-2), by dividing the leaf dry weight by a leaf surface ratio (*LSR*, dimensionless) whose value varies between species. When the last development stage is reached, the green tissues are converted to dry tissues ($DW_{drystem}$, in kg.m-2). The amount of LAI reduction caused by senescence *SLAI* will be used to compute the amount of litter produced by the vegetation cover, named DW_{litter} . DW_{litter} will then degrade at a fixed rate set by the user.

The percentage of surface covered by vegetation (VC) is determined from an exponential relationship with LAI multiplied by k_{VC} , a conversion coefficient which will be determined following the calibration procedure (Eq. 8).

$$\sum_{j=1}^i \sum_{i=1}^j VC_j^i(t) = 1 - \exp^{-k_{VC} \cdot LAI_j^i(t)} \quad (\text{Eq. 8})$$

Cohort height H (in m) is calculated from the overall dry mass DW_{tot} multiplied by two coefficients, DW_{H1} and DW_{H2} , which were extracted from the TRY database (Kattge et al., 2020; Eq. 9).

$$\sum_{j=1}^i \sum_{i=1}^j H_j^i(t) = DW_{H1}^i * DW_j^i(t)^{DW_{H2}^i} \quad (\text{Eq. 9})$$

- 2. Water

Infiltration, runoff, and drainage computations are all described in the article introducing the WaLIS model (Celette et al., 2010). Runoff and infiltration are derived from the curve number method as implemented in the SWAT model (Arnold et al., 1998). Surface cover, cumulative rainfall and topsoil water saturation are used to calculate surface runoff. After calculating surface runoff, infiltration will be deduced from the remaining rainfall. After calculating runoff and infiltration, drainage occurs when the compartment is saturated in water, and equals to the surplus amount.

To calculate the effect of vegetation on water friction, the vegetation frontal area per volume a_f (L^{-1}) is calculated for each species (Equation 10). To facilitate the calculation, the effect of each cohort is assumed to be similar to a regular trapezoid facing the water flow, with the width of the upper base L_{sup} equal to the number of individuals in the cohorts multiplied by the area covered by an individual *groundcover* and the percentage of area covered by vegetation. The width of the lower base L_{inf} is derived from L_{SUP} using a dimensionless coefficient k_{shape} set to 2. For the calculation of the seed retention factor, vegetation at the water surface is considered to be contained within a circle of diameter L_{SUP} (Fig. 4).

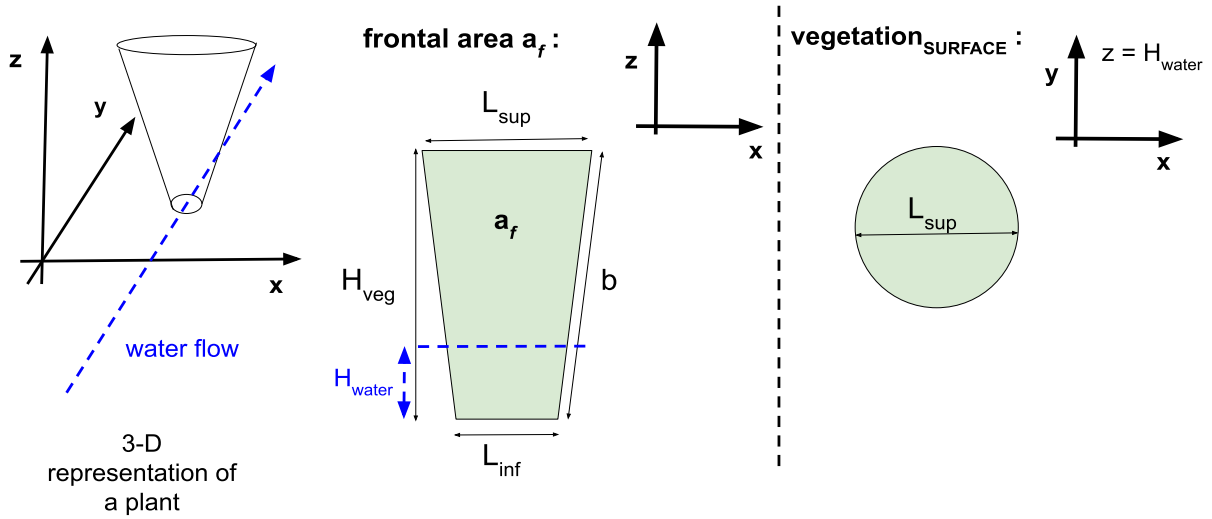


Figure 4. Theoretical representations of the vegetation for the calculation of the frontal area a_f , and the surface of vegetation situated at water level $vegetation_{SURFACE}$.

$$a_f(t) = 0.5 \left(L_{sup_j}^i(t) + L_{inf_j}^i(t) \right) * b_j^i(t) \quad (\text{Eq. 10})$$

The water friction can be derived from this vegetation metric in interaction with the water level by calculating the Manning coefficient K_{man} (dimensionless, Nepf, 2012). When the mean height of the vegetation cover is equal to or higher than the water level, K_{man} varies as a_f and H_{WATER} , in conjunction with the constant drag coefficient C_D and the gravitational force g (Eq. 11). Then, when the vegetation is submerged, K_{man} is also determined by the shear stress coefficient C_x (dimensionless, varying between 0.05-0.13 in field data according to Luhar and Nepf, 2012) and the blockage factor B , which is the ratio of a_f to the total frontal area (Eq. 12). Both equations include the constant K , equal to $1 \text{ m}^{1/3} \cdot \text{s}^{-1}$, which is required to make the equations dimensionally correct.

$$\text{if } H_{water}/H_{veg} \leq 1: 1/K_{man} = \left(0.5 C_D * a_f * H_{water} \right)^{0.5} * \frac{K \cdot H_{water}^{1/6}}{g^{0.5}} \quad (\text{Eq. 11})$$

$$\text{if } H_{water}/H_{veg} > 1: 1/K_{man} = \left[\left(2/C_x \right)^{0.5} * (1 - B)^{-1.5} + \left(\frac{2}{C_D \cdot a_f \cdot H_{veg}} \right)^{0.5} * B \right] * \frac{K \cdot H_{water}^{1/6}}{g^{0.5}} \quad (\text{Eq. 12})$$

Seed retention (in %) by vegetation can be determined using the surface of vegetation at the water level, noted $vegetation_{SURF}$ (in m^2), coupled with the frontal area a_f , the Reynolds number \mathcal{R} (dimensionless), and the length of the section over which water flows l (Eq. 13; Rudi et al., 2021).

$$seed\ retention(t) = 1 - \exp^{\frac{-vegetation_{surf}}{a_f(t) \cdot \mathfrak{R} \cdot 10^{-5} \cdot l}} \quad (\text{Eq. 13})$$

- 3. Representation of soil and ditches management practices

During a mowing event, only cohorts whose height exceeds the mowing height will be affected. The mowing height has been set to 1 cm following discussions with farmers.

Herbicide application is integrated in two different ways, to take into account either the effect of a pre-emergence treatment or a post-emergence treatment. When a pre-emergence treatment is simulated, no germination can occur during the next 145 days. The duration of the germination delay is set by the user. The post-emergence treatment will reduce the LAI by a fixed coefficient during 2 weeks after the day of application, and force the GLAI to 0 for the day of application.

Dredging and eco-burning are practices only applicable to ditches. Dredging is an operation consisting of leveling a strip of earth a few centimeters wide using a backhoe on the ditch to remove the vegetation present and expose the soil. The dry masses will also all be reset to zero, as will the quantity of ash and the values associated with the dry masses (i.e. FVC, LAI, height). Eco-burning is defined by the complete destruction of all dry masses and the production of ash, the quantity of which is determined by the sum of the dry masses burnt multiplied by an ash conversion coefficient.

Lastly, tillage is only applicable during interrow/vine simulation scenarios, and is assumed to have the same effects as dredging.