Phenology of seed ripening, release and wind dispersal

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1 Summary

Phenology is the study of periodic life cycle events of living organisms and how these are influenced by environmental factors such as climate. Late phenological phases such as the timing of seed release and subsequent seed dispersal considerably affect ecology and evolution in plants. Compared to early phases such as leaf unfolding or flowering, late phases like seed ripening and dispersal are far less conspicuous, hard to define and hard to measure, so they have been less widely investigated. Since plants are mostly sessile organisms, seed dispersal is a crucial life cycle event for the ecology and evolution of plants. In fact, long-distance seed dispersal (LDD) is a very complex process in plant biology and significantly shapes the spatial and temporal dynamics of plant populations. For example, wind is a dispersal vector that is important for the spatial spread of many plant species. Wind dispersal in plants is influenced by a variety of factors such as plant traits, habitat type and environmental conditions (e.g. wind speed). Considering the variability of wind conditions throughout the year, the timing of seed release and dispersal is known to have considerable effects on LDD. Taking this seasonal variability in wind conditions into account it can be assumed that wind-dispersed plant species show a synchronisation between dispersal and favourable wind conditions. So far, synchronisation of dispersal conditions and timing of seed release has mainly been addressed in studies focussing on plant species from tropical regions. Even though late phenologies such as ripening duration and timing of seed release and subsequent dispersal are vital in estimating ecologically highly relevant LDD, these phenologies are not appropriately addressed in ecological research. The aim of this thesis is to gain insights into the factors that shape late plant phenologies. In particular, we address the following questions: which ecologically or evolutionary parameters drive the ripening process of plant species? Could the identification of the relevant parameters for seed ripening help project the seed maturity times of species? When do wind-dispersed plant species shed their seeds? How does the seasonal variability of wind affect the seed release phenology of plant species? In view of the variety of factors influencing LDD by wind: how do these factors interact for plant species in different habitat types? How does seed release phenology contribute to the enhancement of LDD by wind?

In order to address these questions, we applied different methodological approaches, ranging from field work and monitoring phenology to computational simulation studies and statistical modeling. To study the ripening process of species, we monitored the flowering, ripening and seed release phenology of more than 100 Central European plant species. Further, to evaluate within-species variability in ripening patterns, we monitored 18 species at three sites along an elevational gradient. We conducted computational simulation studies for estimating LDD by wind based on a broad data set to study the phenology of seed release and the parameters determining LDD by wind. In conjunction with phenological data from literature, we used the obtained simulation results to investigate evidence for the existence of phenological adaptations towards LDD in 165 plant species. Further, we used the results from simulation studies of LDD by wind to disentangle the effects of species, habitat types and meteorological conditions and their interactions on the spatial spread of plant species.

The results of the relationship between plant traits, phylogeny, the ripening process and climatic factors provide insights into the basic understanding of the ripening process of plants. We identified ecological factors that shape species' ripening phenology and seed release timing. In particular, we found a strong statistical relationship between the species' seed weight and the temperature demands for ripening of the seeds. We found that species' seed weight, the ripening process and timing of seed release are tied to the evolutionary history of the species. As a consequence of the phylogenetic signal for seed weight and the positive statistical relationship between seed weight and the duration of the ripening process, we suggest that the species' phylogeny shapes ripening and seed release phenology. With our developed models, we significantly contribute to the understanding of ecological and environmental factors shaping late phenologies. With the statistical models on species' temperature demands for reproduction, we introduce data that that are well suitable for parametrization and further development of plant dispersal models. The results from the elevational gradient study indicated that species possess adaptive potential for physiological needs to produce mature seeds. Our study addresses plant-environment interactions on a spatiotemporal scale that, until now, has only rarely been addressed in plant phenology. To our knowledge, our study is the first approaching single-flower phenology on a multi-species level in Central Europe and thereby provides fundamental insights into the ecological and evolutionary basis of ripening and seed release. Results from independent studies revealed preferential seed abscission during periods with favourable conditions for seed dispersal. Results from monitoring single-flower development from blossom to seed release indicated that herbaceous species with high wind-dispersal potential show seed release during periods with low humidity. By contrast, the results from the simulation study based on a seasonal perspective showed somewhat different patterns: here, heavier seeded tree species with medium wind dispersal potential (including species from the genera *Abies, Acer, Fraxinus* and *Larix*) showed a clear synchronisation of seed abscission with periods favouring LDD. These species, which are both ecologically and economically important, showed significant synchronisation of the highest rate of seed release with high wind-speed that promoted LDD by wind in wintertime. For the tree species mentioned, we suggest interpreting strong seasonal synchronisation as evidence for the existence of phenological adaptations in order to match favourable conditions during seed release. Surprisingly, light-seeded species with high wind dispersal potential showed no apparent seasonal synchronisation of seed release. We suggest that synchronisation with favourable conditions is likely to occur on a shorter temporal scale and that their high potential for wind dispersal allows considerable uplift in each month of the year. With a closer look at the wind conditions that promote LDD by wind, our results showed considerable differences in how specific wind conditions (thermally driven updrafts vs. horizontal wind speed) affect LDD in different species and habitat types. We suggest that LDD by wind in species from open habitats with high wind dispersal potential (e.g. species with plumed seeds from the Asteraceae family) is likely to be driven by thermal updrafts that are mainly driven by the sun providing energy to the ground. By contrast, LDD of heavier-seeded species from open and forested habitats is more likely to be driven by storms that produce shear-driven turbulence.

The results obtained on factors driving ripening and release phenology provide valuable insights into their ecological and phylogenetic factor constraints. The model developed for seed ripening is suggested as a first step in projecting species' seed maturation timing and as a further development of existing computational seed dispersal models. The implementation of more realistic assumptions in assessing species' dispersal potential throughout the year could help considerably in improving landscape management (e.g. timing of mowing) and in the conservation of plant populations. To my knowledge, the study conducted on seasonal synchronisation between seasonal seed release timing and favourable conditions for LDD by wind is the first that comprehensively addresses this relationship applying a multi-species approach considering species from regions with a temperate climate. The evidence found for phenological adaptations towards LDD in plants is an important step in understanding the evolutionary basis of LDD in these species.

Our results on the effect of environmental and ecological factors influencing species' LDD by wind show considerable differences in how updrafts and horizontal wind speed affects LDD between different species and habitat types. Hence, these results help considerably in disentangling the variety of processes involved in shaping diaspore transport over longer distances. The results from this thesis contribute to an increased understanding of the complete dispersal process of plants and to making more realistic projections of (future) plant distribution. The outcomes concerning the role of phenology in shaping LDD and impacting its evolution show that future work should devote increased attention to late phenological phases in plants.

2 Zusammenfassung

Die Phänologie befasst sich mit den im Jahresverlauf periodisch wiederkehrenden Erscheinungen in der Natur. Sie ist die Lehre vom Einfluss des Wetters, der Witterung und des Klimas auf den jahreszeitlichen Entwicklungsgang von Lebewesen. Im Pflanzenreich beschreibt die Phänologie den zeitlichen Verlauf von Blatt-, Blütenentfaltung und vegetatives Wachstum (sogenannte frühe phänologische Phasen) sowie von reproduktiven Phasen wie Diasporenreife, -ausstreu und -ausbreitung (sogenannte späte Phasen). Diese späten phänologischen Phasen sind sehr wichtige Ereignisse im Lebenszyklus von Pflanzen und tragen entscheidend zu ihrem reproduktiven Erfolg bei.

FORSCHUNGSSTAND ZUR PFLANZENPHÄNOLOGIE

Obwohl die bedeutende Rolle der späten phänologischen Phasen in der wissenschaftlich-ökologischen Literatur weithin anerkannt ist, wurden bislang weitaus weniger Studien über späte Phasen als über frühe Phasen publiziert. Zu dieser Unterrepräsentanz von späten Phasen tragen unter anderem folgende Eigenschaften der späten jahreszeitlichen Entwicklungsschritte bei: Späte Stadien sind aufgrund ihrer zumeist geringeren Auffälligkeit während praktischer Feldarbeit weniger leicht zu entdecken. Dies gilt insbesondere für krautige Pflanzen und lässt sich hier einfach an dem Vergleich der Auffälligkeit von Blüten und eher unscheinbaren Diasporen illustrieren. Im Allgemeinen fällt das Differenzieren einzelner Entwicklungsschritte bei späten Phasen (z.B. das Reifen und die Ausbreitung von Diasporen) schwerer als das Ansprechen aufeinanderfolgender Entwicklungsstadien bei frühen Phasen (z.B. Knospung, Blattentfaltung und Blüte). Die genannten Charakteristika haben zur Folge, dass die phänologischen Phasen des Reifens von pflanzlichen Diasporen bisher wenig verstandene Prozesse in der ökologischen Forschung geblieben sind. Es ist beispielsweise wenig über die relativen Einflüsse von ökologischen Faktoren wie Diasporenmerkmalen oder des Verwandtschaftsgrades verschiedener Pflanzenarten auf die Dauer des Reifeprozesses bekannt. Auch die Ausbreitung von Diasporen, etwa im Fell und Verdauungstrakt von Tieren oder durch Wind, ist aufgrund der bereits oben angesprochenen Limitationen in der Feldarbeit empirisch schwer zu erfassen.

FORSCHUNGSSTAND ZUR AUSBREITUNG VON PFLANZEN

Die sessile Lebensweise adulter Pflanzen bringt es mit sich, dass der Transport ihrer Diasporen weg von der Mutterpflanze hin zu räumlich entfernteren Habitaten von hoher Wichtigkeit für die Ökologie und das Überleben von Pflanzenpopulationen ist. Besonders der sogenannte Ferntransport von Pflanzendiasporen, welcher vornehmlich während selten auftretender (Extrem-)Ereignisse geschieht, ist hierbei von herausragender Bedeutung für die zeitliche und räumliche Dynamik des geographischen Vorkommens von Pflanzenarten. So ist etwa der Wind für viele Pflanzenarten ein effizientes und überlebensnotwendiges Ausbreitungsmedium.

FERNTRANSPORT DURCH WIND

Im Rahmen der vorgelegten Arbeit wird ein besonderes Augenmerk auf Windausbreitung gelegt, weshalb diese im Folgenden genauer vorgestellt wird.

Windausgebreitete Pflanzenarten haben zur Herabsenkung der Fallgeschwindigkeit ihrer Diasporen oftmals vielfach gestaltete morphologische Anpassungen, wie etwa behaarte (z.B. Löwenzahn, Pappel) oder geflügelte Diasporen (z.B. Ahorn, Esche). Neben diesen Diasporenmerkmalen beeinflussen Pflanzenmerkmale, wie die Höhe der Diasporenausstreu über dem Erdboden und Landschaftscharakteristika, wie die Topographie und der Habitat-Typ, die Qualität der Ausbreitung. Innerhalb eines Habitat-Typs unterscheidet sich die Qualität der Ausbreitung abhängig von dem speziellen Ort der Ausstreu der Diasporen. Solche, die oberhalb einer dichtgeschlossenen Baumkrone freigesetzt werden, erzielen höhere Ausbreitungsdistanzen als Diasporen, welche sich innerhalb der Vegetationskörper ausbreiten. Den genannten Faktoren wird in der wissenschaftlichen Literatur ein hoher Stellenwert für das Ausmaß des Ferntransportes von Pflanzendiasporen beigemessen. Da sich existierende Studien zur Windausbreitung oftmals nur mit der Untersuchung weniger Pflanzenarten, ausgesuchter Habitat-Typen oder kurzer Jahreszeiträume befassen, ist der relative Beitrag der genannten Faktoren zu dem Ausmaß des Ferntransportes nur schwer zu quantifizieren.

EVOLUTION DES FERNTRANSPORTS

Aufgrund der bereits genannten Seltenheit der Ausbreitungsereignisse über größere Distanzen wird Ferntransport im Allgemeinen als ein Prozess beschrieben, der nur sehr schwer zu messen, abzuschätzen und statistisch zu beschreiben ist. Dieser besondere Charakter des Ferntransports hat zu einer regen wissenschaftlichen Diskussion über den Einfluss natürlicher Selektion auf ausbreitungsrelevante Pflanzenmerkmale geführt. So wurde die Rolle weithin anerkannter morphologischer Merkmale, welche das Ausbreitungspotential augenscheinlich erhöhen (z.B. Haken an Diasporen für eine effizientere Ausbreitung im Fell von Tieren), im Zusammenhang mit der assoziierten Seltenheit der Ausbreitungsereignisse diskutiert und vereinzelt in Frage gestellt. Jüngst ist im Zuge dieser Debatte möglicherweise ein zusätzlicher positiver Effekt von natürlicher Selektion auf die Pflanzenphänologie bzw. den spezifischen Ausbreitungszeitpunkt vorgebracht worden: Die Einflussgröße natürlich selektierter morphologischer und phänologischer Charakteristika auf die Steigerung des Ferntransportes ist ein derzeit vielerorts diskutiertes Forschungsfeld in der Pflanzenökologie.

Die für den Ferntransport wichtigen Extremereignisse treten in den verschiedenen Jahreszeiten mit unterschiedlicher Wahrscheinlichkeit auf. Folglich hat neben den oben genannten Landschaftseigenschaften und Pflanzenmerkmalen ebenfalls der genaue Zeitpunkt der Diasporenausstreu und anschließender Ausbreitung von der Mutterpflanze einen großen Einfluss auf das Ausmaß des Ferntransportes. Im Hinblick auf dessen Steigerung erscheint daher für windausgebreitete Pflanzenarten das Vorhandensein von evolutiven Anpassungen an günstige Windbedingungen während des Ausbreitungszeitpunkts als wahrscheinlich. Der genannte Effekt des Zeitpunkts der Diasporenausstreu auf das Ausmaß des Ferntransports wurde bislang in wenigen Studien (mit vornehmlichem Fokus auf tropische Arten) untersucht, in diesen aber als wichtig erachtet. Trotz der oben genannten Einschätzung der Bedeutung der Phänologie von Diasporenreife und -ausbreitung sind die ökologisch-evolutiven Grundlagen der Kopplung von späten phänologischen Phasen und der Qualität des Ferntransportes bislang nur selten in Regionen mit gemäßigtem Klima untersucht worden.

HERAUSFORDERUNGEN FÜR UNTERSUCHUNGEN ZUM FERNTRANSPORT VON PFLANZEN

Die optische Unauffälligkeit windausgebreiteter Pflanzendiasporen führt zusammen mit der Größe vielmals zurückgelegter Ausbreitungsdistanzen dazu, dass pflanzliche Ausbreitungsereignisse nur bedingt empirisch erfasst werden können. Das Erfassen erreichter Ausbreitungsdistanzen erfordert daher spezielle methodische Ansätze, wie das Aufstellen von Diasporenfallen im Feld oder das Durchführen komplexer Computersimulationen. In Folge der speziellen Herausforderungen für die Untersuchung existiert für späte phänologische Phasen ein hoher Forschungsbedarf. Existierende Studien, welche sich der Windausbreitung annehmen, sind vielmals auf die Analyse spezieller Aspekte, wie die Untersuchung der Ausbreitungspotentiale weniger Pflanzenarten, zugeschnitten. Dieser enge Fokus vieler bisher publizierter Studien erschwert Aussagen, Analysen und Vergleiche des Ausbreitungspotentials in Bezug auf ökologisch relevante Faktoren. So fehlen den meisten existierenden Studien experimentelle Ansätze, welche vergleichende Betrachtungsweisen der Ausbreitungsdistanzspektren zwischen unterschiedlichen Pflanzenarten, Habitat-Typen und Windbedingungen erlauben. Die Seltenheit der für den Ferntransport wichtigen Ereignisse sowie die methodischen Schwierigkeiten beim Erfassen dieser führen in Kombination zu einer spärlichen Datenlage, welche die Einordnung und Abschätzung ökologisch relevanter Faktoren erschwert.

ZIELSETZUNG, FORSCHUNGSRELEVANZ UND METHODIK DER VORGELEGTEN STUDIE

Die hiermit vorgelegte Arbeit hat zum Ziel, Einblicke in die ökologischen Hintergründe von späten phänologischen Phasen zu ermöglichen und grundlegende Erkenntnisse über die Phänologie des Reifeprozesses, der Diasporenausstreu und der Diasporenausbreitung darzustellen. Sie will damit vorhanden Forschungslücken schließen und Impulse für zukünftige Untersuchungen geben. Die Arbeit basiert auf der Untersuchung (i) des Reifeprozesses von Pflanzendiasporen, (ii) des saisonalen Aufeinandertreffens günstiger Windbedingungen und (iii) der Ausbreitung der Pflanzendiasporen durch Wind.

(I) DER REIFEPROZESS VON PFLANZENDIASPOREN

In dieser Arbeit untersuchen wir, welche ökologisch-evolutiven Faktoren den Reifeprozess von Pflanzen steuern. Genauer untersuchen wir die relativen Einflüsse und Interaktionen von klimatischen Faktoren (insbesondere Temperatur), Pflanzenmerkmalen, wie beispielsweise das Diasporengewicht, Lebensformen, wie etwa krautige oder strauchförmige Pflanzengruppen, oder aber von Verwandtschaftsgraden und der evolutiven Geschichte von Pflanzenarten.

Der Großteil publizierter pflanzenphänologischer Untersuchungen basiert auf Datensätzen großer landschaftlicher Ausschnitte oder zeitlicher Skalen. Die Ergebnisse sind in der Folge zwar relativ robust, können aber aufgrund der Vielzahl modifizierend wirkender Faktoren (z.B. Mikroklima, Unterschiede zwischen Populationen) nur schwer auf einen einzelnen Faktor (z.B. Einfluss von Temperatur) bezogen werden. Um dieser methodisch bedingten Messungenauigkeit entgegenzutreten, wählten wir bei den phänologischen Studien die einzelne Blüte als Untersuchungsobjekt und führten ein umfassendes Monitoring zur Phänologie der Blüte, Reife und Ausstreu an 104 mitteleuropäischen Pflanzenarten im Botanischen Garten Frankfurt am Main durch. Um den Einfluss klimatischer Parameter auf den Verlauf der Entwicklungsschritte der individuellen Blüten abschätzen zu können, wurden die phänologischen Daten in Bezug auf Temperatursummen, Luftfeuchte und Sonnenscheindauer ausgewertet. Um die phänologische innerartliche Variabilität zu untersuchen, führten wir eine zusätzliche Vergleichsstudie an 18 Pflanzenarten entlang eines Höhengradienten im Vogelsberg (Hessen) durch.

(II) ZEITLICHES AUFEINANDERTREFFEN GÜNSTIGER WINDBEDINGUNGEN UND DER DIASPORENAUSSTREU

In welchem Maße morphologische oder auch phänologische Charakteristika von Pflanzen zur Steigerung der Ausbreitungsdistanzen beitragen können, ist eine in der ökologischen Forschung rege diskutierte Fragestellung. Im Rahmen dieser Arbeit untersuchten wir daran anschließend, inwiefern das saisonale Aufeinandertreffen günstiger Windbedingungen und des Zeitpunktes der Diasporenausstreu den Erfolg der Diasporenausbreitung (in Form von Ausbreitungsdistanzen) beeinflusst. Zum einen führten wir Simulationsstudien mit dem existierenden Computerprogramm PAPPUS durch, um die pflanzenartspezifischen Ausbreitungsdistanzen in Offenland- und Wald-Habitaten im Jahresverlauf zu quantifizieren. Für die entsprechenden Computersimulationen wählten wir eine breite Datengrundlage an Wind-Daten aus drei Jahren. Um Hinweise auf eine mögliche Synchronisierung günstiger Bedingungen für Windausbreitung und des Zeitpunktes der Diasporenausstreu zu erlangen, sammelten wir zum anderen phänologische Daten über den Zeitpunkt der Diasporenausstreu von 125 Offenland- und 40 Waldarten und analysierten diese gemeinsam mit den Ausbreitungsdistanzspektren.

(III) AUSBREITUNG VON PFLANZENDIASPOREN DURCH WIND

Schließlich untersuchten wir den Prozess der Ausbreitung von Pflanzendiasporen durch Wind und inwiefern ökologische, meteorologische und landschaftliche Faktoren diesen Prozess einzeln und in ihrer Interaktion beeinflussen. Insbesondere untersuchten wir in dieser Studie das Zusammenspiel relevanter Diasporen-, und Pflanzenmerkmalen mit verschiedenen Windbedingungen (thermische Aufwinde vs. horizontale Windgeschwindigkeiten) in unterschiedlichen Habitat-Typen und Jahren. Die durchgeführten Computersimulationen bezogen sich auf 36 virtuelle Modell-Pflanzenarten in offenen und bewaldeten Habitaten.

Anders als in vielen bereits publizierten Studien zur Windausbreitung ist in der hier vorgelegten durch den Einbezug der Vielzahl an steuernden Faktoren eine relative und vergleichende Abschätzung ihres Einflusses auf den Ferntransport durch Wind möglich. Um die Simulationsergebnisse zwischen den genannten Untersuchungsvariablen auf vergleichbare Wind-Daten bzw. Zeiträume zu beziehen, wurden für Vergleiche zwischen den Habitat-Typen, Jahren und den Windbedingungen eigens zusammengestellte Datensätze verwendet.

ERGEBNISSE DER ARBEIT

Unsere Untersuchungen haben sowohl für zukünftige Forschungsvorhaben in der Pflanzenphänologie und Ausbreitungs- und Evolutionsbiologie als auch für Anwendungen im praktischen Feld, wie etwa dem Naturschutz, wertvolle Resultate hervorgebracht. Im Folgenden werden jene vorgestellt, die wir als besonders relevant erachten.

(I) INTERPRETATION DER ERGEBNISSE ZUM REIFEPROZESS

Die Ergebnisse zu den Einflüssen von Pflanzenmerkmalen, Pflanzenverwandtschaft, Lebensformen und klimatischen Faktoren (gemessen als Temperatursummen über den Entwicklungsverlauf von Blüte zur Ausstreu) geben prinzipielle Einblicke in den Reifeprozess wilder Pflanzenarten. In unserer Studie identifizierten wir für die Reife- und Ausstreuphänologie zahlreiche relevante ökologische Faktoren. Als besonders hervorstechender Faktor soll hier das Diasporengewicht genannt werden, welches einen hochsignifikanten Einfluss auf die zur Diasporenreife benötigten Temperatursummen hatte. Interessanterweise war dieser statistische Zusammenhang stark von dem Einbezug der unterschiedlichen Lebensformen abhängig. Die phylogenetische Verwandtschaft der 104 untersuchten Pflanzenarten hatte ebenso einen klaren statistischen Effekt auf das Diasporengewicht, den Reifeprozess und den Zeitpunkt ihrer Diasporenausstreu. Das Monitoring der Reife- und Ausstreuphänologie auf drei verschiedenen Höhenstufen im Vogelsberg (110, 250 und 690 m über NN) zeigte, dass die Temperatursummen, welche zur Produktion reifer Pflanzendiasporen notwendig sind, zwischen den untersuchten Pflanzenpopulationen unterschiedlich waren. Pflanzenindividuen, welche auf der höchsten Höhenstufe untersucht wurden, zeigten signifikant geringere Bedarfe an Temperatursummen als solche auf der untersten Höhenstufe. Dieses Ergebnis kann vorsichtig als Indikation für das Vorhandensein eines evolutiven Anpassungspotentials von Arten an die, für die Diasporenproduktion benötigten Temperatursummen interpretiert werden.

Die in dieser Arbeit gefundenen Ergebnisse zur Reifephänologie von Pflanzen und den sie steuernden Parametern sind ein Grundstein für die Weiterentwicklung von statistischen Modellen zur Projektion des Reifezeitpunktes von wilden Pflanzenarten. Ein solches Modell zur Projektion des Reifetermins in Abhängigkeit von beispielsweise Diasporengewicht, Blühzeitpunkt und Lebensform würde einen Gewinn für die ökologische Forschung darstellen. Genauere und artspezifische Einschätzungen des Reifetermins von Pflanzenpopulationen würden etwa die Wahl des Mahdtermins in Hinblick auf naturschutzrelevante Fragen, wie den Erhalt der Diasporenbank, unterstützen und erleichtern. Andererseits spielt der Reifezeitpunkt invasiver Pflanzenarten eine Rolle für den Erfolg ihrer Kolonisierung neuer Regionen und könnte bei der Wahl des Zeitpunkts von Naturschutzmaßnahmen (beispielsweise beim Entfernen fruchtender Individuen) helfen. Ein methodisches Manko anderer Simulationsprogramme ist, dass diese zur Modellierung der Ausbreitung von Pflanzen, etwa durch Wind, Zeiträume berücksichtigen, welche nicht den natürlich vorkommenden Ausbreitungsperioden der jeweiligen Pflanzenarten entsprechen. Durch die Weiterentwicklung des in dieser Arbeit berechneten statistischen Modells zur Ermittlung des Zeitpunktes der Diasporenreife könnte die Aussagekraft und Realitätsnähe existierender Modelle zur Ausbreitungsbiologie deutlich erhöht werden.

(II) INTERPRETATION DER ERGEBNISSE ZUR ZEITLICHEN SYNCHRONISATION GÜNSTIGER WINDBEDINGUNGEN UND DER DIASPORENAUSSTREU

Im Rahmen dieser Arbeit wurden durch den Einsatz unterschiedlicher zeitlicher Auflösungen und Untersuchungsobjekte (einzelne Blüten vs. klassische Phänologie-Daten aus der Literatur) in den durchgeführten Studien verschiedene Formen des Aufeinandertreffens günstiger Ausbreitungsbedingungen und der tatsächlichen Diasporenausstreu entdeckt. Das durchgeführte Monitoring zur Blüh- und Reifephänologie auf Einzelblüten-Ebene zeigte, dass die Diasporenausstreu von krautigen Arten mit einem hohen Windausbreitungspotential vornehmlich während lufttrockenerer Perioden stattfindet. Hingegen lassen die Ergebnisse aus der Studie, in welcher Computersimulationen zum Ferntransport mit phänologischen Daten über den Zeitpunkt von Reife und Diasporenausstreu kombiniert wurden, einen anderen Schluss zu: Für ökologisch und ökonomisch wichtige Baumarten mit mittlerem Windausbreitungspotential (Baumarten der Gattungen Tannen, Ahorne, Eschen und Lärchen) scheinen speziell die Wintermonate mit hohen Windgeschwindigkeiten von großer Bedeutung zu sein. Für diese Pflanzengruppe mag natürliche Selektion eine jahreszeitliche Verspätung des Zeitpunktes der Diasporenreife und der Diasporenausstreu erwirken, und die Ausbreitung durch Wind vornehmlich in der stürmischeren Winterzeit stattfinden lassen. Das zeitliche Aufeinandertreffen von Diasporenausstreu und hohen Windgeschwindigkeiten während Winterstürmen kann also als ein Vorhandensein phänologischer Anpassungen der Diasporen an Ferntransport gedeutet werden. Für Pflanzenarten mit einem hohen Windausbreitungspotential hingegen (beispielsweise krautige Arten aus der Familie der Korbblütler oder Baumarten der Gattungen Pappeln und Weiden) zeigen die Ergebnisse, dass Diasporentransport über längere Distanzen während des gesamten Jahresverlaufes wahrscheinlich ist. Für diese Arten scheint das Fehlen eines saisonalen Aufeinandertreffens der Diasporenausstreu und des Ferntransportes ein Indiz für Mechanismen zu sein, die während kurzfristiger Wetterereignisse (beispielsweise rasch auftretende Lufttrockenheit) wirksam sind. Zusammenfassend kann angenommen werden, dass mit Abnahme des Windausbreitungspotentials die Rolle der Windausbreitungsphänologie steigt.

Die in dieser Arbeit bei unterschiedlichen Pflanzengruppen erkannten divergenten Muster in der jahreszeitlichen Verteilung optimaler Zeitfenster für die Windausbreitung zeigen, dass Modelle zur Simulation der Ausbreitung an diese spezifischen Pflanzengruppen angepasst werden sollten. Momentan wird in den meisten verwendeten Ausbreitungsmodellen ein über das Jahr gleichmäßig erfolgender Ferntransport zugrunde gelegt. Weiterhin stellen die Ergebnisse zu dem Einfluss der Phänologie der Diasporenausstreu auf den Ferntransport einen wichtigen Beitrag zur Frage der Evolution des Ferntransportes dar.

(III) INTERPRETATION DER ERGEBNISSE ZUR WINDAUSBREITUNG

Die Ergebnisse zur Windausbreitung geben Aufschluss über bislang wenig untersuchte Interaktionen zwischen Landschaftsaspekten, Windbedingungen und Pflanzenmerkmalen. Das Ausmaß des Ferntransports war oberhalb des Blätterdaches von Wäldern höher als über der Offenland-Vegetation, hingegen hatte auf ebendiesen die Fallgeschwindigkeit in beiden untersuchten Habitat-Typen einen großen Einfluss. Die Höhe der Samenausstreu über dem Erdboden wiederum war allein im Offenland ein wichtiger Faktor. Im Vergleich des Ferntransports zweier unterschiedlicher Jahre waren die Unterschiede für Waldarten größer als im Offenland. Ein genauerer Blick auf die für die Windausbreitung wichtigen Wind-Parameter zeigt, dass spezifische Bedingungen wie thermische Aufwinde oder hohe Windgeschwindigkeiten die Fernausbreitung von Pflanzen in Offenland- und Wald-Habitaten unterschiedlich stark beeinflussen. Für Offenlandarten gibt es einen positiven Effekt von thermischen Aufwinden auf den Diasporen-Ferntransport. Für Offenland- und Waldarten mit einem mittleren bis niedrigen Windausbreitungspotential hingegen scheinen Sturmereignisse mit höheren Windgeschwindigkeiten einen hohen Einfluss auf den Ferntransport zu haben. Unsere Ergebnisse zeigen damit klare Unterschiede in Bezug auf die Rolle von spezifischen Windbedingungen (Aufwinde vs. horizontale Windgeschwindigkeiten) für unterschiedliche Pflanzenarten in Offenland- und Waldhabitaten. Bislang sind solche umfassenden Studien zur Windausbreitung nur selten durchgeführt worden und erschwerten aufgrund der Verwendung nicht-identischer Simulationsprogramme oder abweichenden experimentellen Designs vergleichende Aussagen. Dank des breiten Spektrums der ausgewählten Modellarten, Einbezug von Offen- und Waldhabitaten, sowie der Verwendung unterschiedlicher Kalenderjahre an meteorologischen Daten, stellen unsere Ergebnisse einen wertvollen Beitrag zu der wissenschaftlichen Auseinandersetzung der relativen Bedeutung windausbreitungsrelevanter Einflussgrößen dar.

ZUSAMMENFASSUNG UND AUSBLICK

Die vorgelegte Arbeit umfasst die aufeinanderfolgenden späten Ereignisse der Reife, Diasporenausstreu und Ausbreitung im Lebenszyklus von Pflanzen. Mit den in dieser Studie präsentierten Ergebnissen zur Phänologie von Reife und Ausstreu vertiefen wir wissenschaftlich fundierte Einblicke in deren ökologischen und evolutiven Grundlagen. Mit den hierfür entwickelten Modellen stellen wir zudem eine Grundlage zur Weiterentwicklung und Parametrisierung von Modellen zur Projektion des Termins von Reife und Ausstreu wilder Pflanzenarten bereit. Durch die Ergebnisse zur Rolle der Phänologie für die Steigerung der erzielten Ausbreitungsdistanzen stimulieren wir die wissenschaftliche Debatte über die evolutiven Grundlagen des Ferntransportes. Der Einbezug unterschiedlicher Pflanzenarten aus Offenland- und Waldhabitaten sowie eine umfassende Grundlage and verwendeten Winddaten erlaubt eine Einschätzung für die pflanzengruppenspezifisch unterschiedlich stark ausgeprägte Rolle der Landschaftscharakteristika, spezifischen Windbedingungen, Pflanzen- und Diasporenmerkmalen, sowie der Phänologie der Ausstreu für die Steigerung des Ferntransports durch Wind. Zusammenfassend nehmen wir an, dass die Rolle von phänologischen Anpassungen an den saisonalen Zeitpunkt der Diasporenausstreu mit Abnahme des Windausbreitungspotentials an Bedeutung gewinnt. Im Allgemeinen empfehlen wir späte phänologische Phasen für zukünftige Studien rezenter ökologischer Forschung stärker zu berücksichtigen und vor dem Hintergrund der aus der vorgelegten Arbeit gewonnen Erkenntnisse weithin angewandte Modelle zur Kolonisierung zukünftiger Habitate erneut zu evaluieren und weiterzuentwickeln.

3 Preface

The timing of offspring dispersal is vitally important for the reproductive success in many organisms such as mammals, birds, insects and plants. In plants, the phenologies of both seed ripening and seed release affect various aspects in plant biology as for instance the rate of spatial population spread, reproductive success and the survival of species.

The three studies presented in this thesis comprise three important processes involved in reproduction, namely seed ripening, seed release timing and seed dispersal. These mentioned processes addressed in the framework of this thesis are linked to another in a rich interplay of plant traits and e.g. the species' life form. The aim of this thesis is to characterise and identify plant traits that control the ripening process (section 8.1, project i on page 76 ff.), the role of seed release timing for different plant groups (section 8.2, project ii on page 120 ff.) and the role of plant traits and weather conditions for dispersal of plant seeds (section 8.3, project iii on 154 ff.). For a summary of the main characteristics of the different projects comprised in this thesis, please see Table 1 on page 39.

Firstly, I start with a general introduction on seed dispersal and plant phenology. In this section, I describe the current knowledge on dispersal and subsequently concentrate on dispersal by wind. I outline general aspects in plant phenology in temperate regions and focus on late phases in plant phenology. Further, I highlight the importance of phenology of seed dispersal for ecosystems, reproductive success of species and implications for both plant conservation and climate change. Thereafter, I present each of the three research projects included in this thesis and name the main research questions in each particular research field.

Secondly, I present and summarise the most relevant findings that were obtained in the studies that I conducted together with my colleagues in chapter 5 'Summary of the main results'. Herein, the main findings are presented according to the research questions posed in section 4.5 'Scope of this thesis'. The detailed scientific papers, in which the research projects are presented comprehensively, are provided in the sections 8.1, 8.2, and 8.3.

Thirdly, I integrate my key findings in the current 'state of the art' of phenology research in the comprehensive discussion and illustrate the importance of their implications. I discuss the obtained results with a view to environmental and phylogenetic constraints separately. Subsequently, I reveal the different methodological approaches chosen for each of the three research projects with respect to e.g. the type of the data source, temporal and spatial resolution and the number of species that were considered. Thereafter, I interlink the results obtained in the three projects and comprehensively discuss them considering climate change.

4 General introduction

4.1 Ecology of seed dispersal

4.1.1 Importance and historical background

Seed dispersal strongly affects plant diversity distribution, biodiversity patterns and population dynamics (Nathan et al. 2008; Schupp et al. 2010; Carlo et al. 2013). Dispersal is defined as the movement of individuals from their birth location to another location where they might establish and reproduce (Clobert et al. 2001; Bullock 2002). In the context of habitat fragmentation, land use changes, climate change and biological invasions, the awareness of the prominent role of seed dispersal increases and motivates recent studies that address the ecology and evolution of seed dispersal.

A glance back in research history shows, that seed dispersal received only little attention and was even assumed to be unimportant (see Cousens et al. 2008). Although Charles Darwin pioneered the study of long-distance dispersal (Darwin 1859), it remains as a modern and hardly understood discipline in ecology (Green & Figuerola 2005). For a long period, dispersal research was either anecdotal or speculative (Nathan et al. 2008) and seeking to explain selective values of morphological adaptations possibly related to dispersal (Ridley 1930; van der Pijl 1982). Even during the rise of plant population ecology in the 1970ies, dispersal biology was seldom a focus for research. This neglect of dispersal biology has changed and the scientific community became aware of its importance for fundamental processes in plant ecology and evolution. Today, dispersal is suggested to hold a central role for dynamics and evolution of spatially structured plant populations, to contribute to the genetic integrity of species across space and to track favourable conditions in a changing world (Ronce 2007). Hence, dispersal research has become a central part of ecology research and its importance for pure and applied ecology research is widely acknowledged (Cousens et al. 2008).

Please note, that within the framework of this thesis, I consider seed dispersal to be the phase between seed release from the parent plant until (first) seed deposition at ground level. It is however important to note that processes such as secondary dispersal are not covered by the quantitative and experimental approaches followed in this work. However, these processes are important and can affect spatiotemporal dynamics of some species (see e.g. Greene & Johnson 1997; Hoshizaki et al. 1999; Schurr et al. 2005).

4.1.2 Different vehicles of travelling seeds: dispersal vectors

In higher plants, spatial spread is mostly achieved by dispersal of seeds, although the vegetative or generative dispersal unit can be diverse and e.g. constitute the botanical unit germinule, fruit or even a fragment of the parent plant that contains the dispersal unit. The most frequently involved dispersal vectors are either abiotic (wind and water) or biotic (animals and plants themselves, Levin et al. 2003) with the associated dispersal syndromes: anemochory, hydrochory, zoochory, and autochory, respectively (van der Pijl 1982). Dispersal strategies have important implications for plant populations, communities and thus for evolutionary plant fitness (Levin et al. 2003). Already in the early days of dispersal ecology research, attention was payed towards the linkage between dispersal and its demographic consequences. Since then, various studies focused on that topic (Hamilton & May 1977; Willson & Traveset 2000). Based on the complexity and variety of processes involved in plant dispersal, studies addressing its demographic consequences and evolution are still a challenging field in plant ecology research. Some studies have suggested that the probability for offspring survival increases with increasing dispersal distance from the parent plant: in particular, these studies introduced the ‘escape theory’ for seeds (Janzen 1970; Connell 1971) and stressed the importance of avoidance of ‘kin competition’ (competition amongst individuals of the same species Hamilton & May 1977). Although more distant sites are more might show distinct habitat properties (e.g. in terms of lower nutrient availability or distinct edaphic conditions), more distantly dispersing seeds were suggested to greatly benefit from lower competition and show enhanced offspring survival.

In general, dispersal syndromes are commonly classified on the basis of the existence of apparent morphological adaptations (e.g. winged seeds for wind dispersal, hooked seeds for epi-zoochory and fleshy diaspores for endo-zoochorous dispersal). However, these general classification methods tend to misconstrue important characteristics of the seed dispersal process (Levin et al. 2003) and are therefore questionable (Tackenberg et al. 2003a).

In order to clarify scientific terms related to ripening, I will refer to the term ‘**seed**’ as often used in scientific literature considering dispersal biology. Although generative dispersal units can be diverse and could be more accurately described by referring to specific botanical terms (see van der Pijl 1982), here I use the term seed as a general term for dispersal of a reproductive part of the plant (see also Levin et al. 2003).

The complete process of seed dispersal is rarely mediated by a single dispersal vector and is not limited to the primary movement of the diaspore. Rather, dispersal also includes subsequent movement that can be driven by wind (Schurr et al. 2005) or other dispersal vectors such as animals (Hoshizaki et al. 1999). In general, these different dispersal vectors considerably differ in the spatial patterns of seed deposition (Howe & Smallwood 1982). Seed dispersal through the animal's gut depends on both the seed retention in the digestive tract of the animal vector species and the movement of the animal (endo-zoochorous seed dispersal, Bonn 2005). Likewise, seed dispersal through seed attachment in the animals coat depends on the seed retention on animal's coats and the animal movement (epi-zoochorous dispersal, Tackenberg et al. 2006). Compared to other dispersal types, dispersal by birds is more directional i.e. with higher probabilities for seed deposition in habitats that are similar to those of the mother plant and more suitable for the offspring survival (Carlo et al. 2013). Likewise, hydrochory can result in systematic delivery of seeds to specific types of fluvial environments and is suggested to lead to directed dispersal for riparian plant species (Merritt & Wohl 2002). Wind dispersal is commonly suggested to yield in more unidirectional seed deposition than dispersal by water or animals. However, the proportion of deposited wind-dispersed seeds may be higher e.g. in the prevailing wind direction (Carey & Watkinson 1993). For example, stronger winds that have a dominant direction can lead to more directed dispersal (Greene et al. 2008). Further, higher seed deposition in vegetation gaps is suggested to be a result of air currents that pull wind-dispersed seeds from the surrounding area (Schupp et al. 1989; Wenny 2001).

Quantifying dispersal

The spatial distribution of dispersed seeds around the parent plant is – among others – called 'seed shadow' (Janzen 1971) or 'seed rain' (Wagner 1965; Houle 1998). Further, more statistically based terms and metrics are used in dispersal research: for example the term 'dispersal kernel' which sums discrete probability density functions of dispersal distances (Silverman 1986) and describes the distribution of seed deposition as a function of distance. In general, most seeds move over relatively short distances and only few seeds are dispersed over longer distances (e.g. Willson 1993; Shigesada et al. 1995; Clark et al. 1998). In the distant past, short-distance dispersal (the peak portion of the dispersal kernel where most seeds are deposited) received most attention from ecologists due to its importance as a source of food for predators and other consumers (e.g. Herrera 1984, summarised in Green & Figuerola 2005). Today, the smaller portion that travels over long distances is – according to the current state of the art – widely acknowledged to be ecologically important when referring to evolutionary fitness of the parental generation. Long-distance dispersal (LDD) is widely regarded to affect many fundamental processes like gene flow between populations, local adaptation and spatial dynamics of ecosystems. Please see the introduction in project iii (section 8.3.2) for a detailed description of LDD and it's vital importance for plant ecology.

LDD is differently described and quantified in literature and researchers argue in different directions with respect to the application of specific measures of LDD. For instance, to compare dispersal potentials of different species, the usage of absolute measures that directly address the dispersal distances achieved can be appropriate (Green & Figuerola 2005). On the other hand, when looking at research questions associated to landscape fragmentation, measures that refer to predefined distances (e.g. proportion of dispersal events exceeding the distance of 1000 m) might be much more target aimed than simple absolute measures (Nathan 2005).

In order to gather LDD data, either extensive field work (e.g. by using seed traps) or computational modelling studies e.g. simulating single seed trajectories can be applied. Such modelling approaches are widely applied in studies addressing dispersal ecology and LDD research (e.g. mechanistic dispersal models; Trakhtenbrot et al. 2014; Lönnell et al. 2015). Likewise, within this thesis we used the wind dispersal model PAPPUS (Tackenberg 2003) in order capture ecologically important rare LDD.

Wind as the dispersal vector addressed in this study

The main dispersal vector addressed in this thesis is dispersal by wind. In order to streamline the introduction with respect to the pivotal topics handled within this thesis, I will mostly focus on dispersal by wind in the following. LDD of plant seeds by wind is mainly shaped by landscape characteristics, the prevailing meteorological conditions and both species' seed and plant traits. The focal plant traits that are commonly suggested to promote LDD by wind are seed terminal velocity and the height of diaspore release (e.g. Tackenberg 2003; Soons et al. 2004; Heydel et al. 2014). Many previously published studies that addressed the importance of the mentioned focal factors focussed on one or few plant species only (e.g. Caplat et al. 2012; Zhu et al. 2015), addressed either open landscapes or forests, referred to different time periods or used different simulation models. As a result, the relative importance of these mentioned factors is still under debate and the importance of their variability in vegetation types, sites and years has only rarely been quantified. Within this thesis, the divergent interaction between the species traits seed terminal velocity and height of seed release, different vegetation types, and differences in wind conditions are specifically in project iii (section 8.3) and project ii (section 8.2).

Please note that in project ii and project iii, the species' dispersal potential by wind is mostly referred to as 'seed terminal velocity' (depending on the journals guidelines abbreviated as either V_{term} or VTERM) that is measured in m/s during fall of the seed. Within the common introduction and discussion of this thesis, I will preferably refer to the more intuitive terminology of the 'wind dispersal potential' of species and mostly avoid using the more technical term seed terminal velocity. It is important to note that the terms used in the classification of seed terminal velocity and potential for dispersal by wind are opposing: species with a *low* seed terminal velocity (e.g. *Taraxacum* sect. *Ruderalia* Kirschner, H.Øllg. & Štěpánek) have high wind dispersal potential.

Seed dispersal by wind is greatly influenced by seasonal differences in the specific availability of the dispersal vector wind. Hence, the specific timing of both seed release and subsequent dispersal affects the distances travelled by the seeds (Nathan et al. 2001; Heydel et al. 2015). With regard to such inter-annual differences in dispersal potential, the species-specific periods of seed maturity should be implemented in existing mechanistic dispersal models. For example, the dispersal model PAPPUS applied within this thesis could be modified in a way in which species' dispersal only takes place during the effective species-specific periods of seed release. From the view of community wide patterns, this gain of reality in dispersal modelling could help to considerably improve estimations of existing seed dispersal models.

4.2 General introduction to plant phenology

Phenology is the study that addresses periodic life cycle events of living organisms and how these are influenced by environmental factors such as climate. The term ‘phenology’ is derived from the Greek *phainō,* which can be translated with “to show”, “to bring to light”, or “to appear” (Schwartz 2013). Plant phenology describes the timing of growth and reproductive activity within the year. In general, plant phenologies of species from temperate climates are mainly constrained by seasonality of temperature and moisture availability. The main phenological phases are germination, leaf development, vegetative growth, flowering, ripening, release and senescence. As the first step in the life cycle of a plant, germination is of great importance for success of subsequent establishment and colonization (Thompson et al. 2002). Seedlings have a minimal capacity for lowering their physiological demands in the face of unfavourable abiotic or biotic conditions. As a consequence, the seedling stage is a vulnerable stage in the life cycle of a plant and its timing is likely to be under strong natural selection to occur when conditions are favourable for seedling establishment (Rathcke & Lacey 1985). The initiation of germination is triggered by a remarkable diversity of factors including temperature, moisture, light intensity, photoperiod and carbon dioxide (Rathcke & Lacey 1985; Gurevitch et al. 2006). The relationship between plant phenologies and animals are rather complex. This is due to the fact that for animal pollinators, seed dispersing animals, and herbivores, plants and animals can be agents of selection on each other (Gurevitch et al. 2006).

In the following, I introduce some phases involved in reproductive plant phenology and outline them in the sequence of their appearance. In particular, I examine the evolutionary and environmental factors that contribute to observed processes and temporal patterns of these phases. Furthermore, I put these patterns and processes in the context of how these phases affect subsequent life-cycle events and plant fitness.

4.3 Flowering phenology

Temporal patterns of flowering in plant communities within the season were widely discussed in the past: Clarke (1893) was considered to be the first who devoted a paper to this topic (Inouye & Iler 2012; Waser 2015). In his early work, he proposed a general pattern of seasonal flowering according to the species' evolutionary history. Clarke (1893) proposed flowering to progress from spring through autumn, beginning with more ancestral taxa and terminate with more derived (i.e. evolutionary more advanced) taxa. Only two years later, Robertson (1895) objected to this theory and presented his alternative theory, which today might be interpreted as a scenario of community assembly. In particular, Robertson (1895) emphasized on natural selection that modifies flowering times to match flight times of pollinators (especially in species that are specialised to one functional type like e.g. bumblebees, see Waser 2015). At the same time, natural selection on flowering times was suggested to avoid competition for pollinators and hence facilitate successful pollination (Robertson 1895). Theories from both views primarily referring to either phylogenetic constraints or avoidance of pollination competition were later jointly examined in much-cited publications (Rathcke & Lacey 1985; Kochmer & Handel 1986). Within these studies, the flowering time was suggested to be maintained by natural selection, phylogenetic constraints, and life form whereby phenological events were also suggested to be plastic and able to quickly respond to environmental variation. For initiation of flowering, phylogenetic constraints were later suggested to not simply conserve the specific time of the year, but rather the phenological response to a set of environmental cues (Davies et al. 2013). Due to the fact that the majority of species from a certain plant family still flowers at the same time, absence of natural selection on shifts in flowering time has been suggested (Ollerton & Lack 1992).

The specific timing of flowering can affect various stages in the plant life-cycle. Besides the above-mentioned competition during pollination, subsequent life-cycle events are also affected by the flowering timing. For instance, a flowering phenology that shows two distinct flowering peaks was suggested to reduce the rate of seed predation (Atlan et al. 2010). The specific flowering time can affect the rate of offspring in annuals: for example, delayed flowering was shown to reduce the number of flowering individuals within a plant population (Hamann 2004). In addition to it, the timing of flowering can affect the offspring life-history schedule (annual vs. biennial life form; Galloway & Burgess 2009) and plant fitness (e.g. in the perennial herb *Lathyrus vernus* (L.) Bernh.; Ehrlén & Münzbergová 2009). Likewise, timing of flowering affects the rate of seed ripening (Tukey 1952; Menzel 2003) and was shown to be associated with the fruit maturation time and subsequent fruit removal by birds (Aizen 2003). Despite these examples of effects of flowering timing, we have only little understanding how initiation of flowering generally influences subsequent reproductive phenologies (Galloway & Burgess 2009).

Increases in temperature throughout the season have direct and strong effects on early phenological phases as e.g. timing of leaf flush or flowering (Menzel 2000, 2003). For the timing of flowering, mainly the sum of temperatures experienced over some period of time ('cumulative temperature sum' or 'temperature degree days') and not the specific temperature on a particular day were suggested as *the* important driver (Wielgolaski 1999; Larcher 2003; Menzel et al. 2006). For most plant species from the temperate region, temperature is the pivotal diver for their development whereby other factors such as day-length play a less important role. Plant species whose development is primarily affected by temperature and not by day-length are called 'day neutral' plants (e.g. *Impatiens balsamina* L. or *Poa annua* L.; Lambers et al. 2008). By contrast, flowering timing of many short-lived species (Rathcke & Lacey 1985) is triggered by either short or long days ('short-day' or 'long-day' plants as for instance *Eupatorium cannabinum* L. and *Trifolium pratense* agg., respectively; Lambers et al. 2008).

4.4 Late phenological phases

Late phenological phases such as seed ripening, seed release and subsequent dispersal influence how emerging plants interact with the environment and impact their fitness (Cousens et al. 2008; Ehrlén & Münzbergová 2009). The timing of reproduction has considerable fitness effects in many organisms, including birds (Thomas et al. 2001), insects (Landa 1992) and plants (Galloway & Burgess 2009; Hamann 2004). Even though the importance of timing of late phases for the understanding of factors driving e.g. seed dispersal and the ecologically highly relevant LDD is often highlighted in literature (Nathan et al. 2008), late phases are often neglected in phenological approaches. In general, late phases like seed ripening and dispersal remain much less investigated than for example germination, leaf unfolding or flowering (Sparks & Menzel 2002; Gomez-Aparicio et al. 2007). Late phases are much less conspicuous and harder to differentiate than early phases (e.g. germination, establishment, leaf flush and flowering). This particularly applies to the herbaceous plant species with their much more conspicuous flowers than their comparatively plain diaspores and has led to a much finer and specific differentiation of relevant early phases as it is the case for late phenological phases. In order to enable the comparison and functional analyses of late phenological phases, a much more detailed differentiation of the single phases passed during flowering, ripening, release and dispersal seem important. Thus, it can be summarised that studies explaining general patterns of species' seed ripening phenology are lacking and urgently needed (Rathcke & Lacey 1985) in order to better understand its functional biology. Even in meta-studies, the phenological phase of interest mostly is flowering (Menzel 2003; Menzel et al. 2006). In order to e.g. address questions related to species' potential for dispersal of seeds, empirical methodological approaches are apparently, in most cases, hardly applicable. In most cases, practical and empirical work that assesses the seed's trajectory can either individually track the seed for only few meters or implies the usage of seed traps (e.g. Nathan et al. 1999). However, the ecologically important dispersal events that take place over longer distances (exceeding e.g. hundreds of meters) can hardly be tracked with such empirical approaches. Here, computer simulations that e.g. model single seed dispersal trajectories depict much more applicable methodological approaches and can offer valuable results. In the following sections, I describe the current knowledge in phenology of late phases involved in plant reproduction.

4.4.1 Phenology of ripening

While the phenologies of early phases are suggested to be primarily triggered by temperature (e.g. Wielgolaski 1999; Larcher 2003), seed ripening is believed to be mainly shaped by 'internal' factors (Crane & Brown 1942; Herrera 1984; Rathcke & Lacey 1985). These factors may include plant phylogeny and morphological parameters such as seed size (Primack 1985). By contrast, 'external' factors such as temperature are suggested to additionally modify the seed ripening process (Tukey 1952; Menzel 2003). With the few published articles that address the ecological traits that drive the ripening process from a multi-species perspective in Central Europe, it remains hard to realistically estimate the date of seed maturity of plant species. Previous studies that were carried out by Primack (1985) and Jia et al. (2011) addressed the seasonal timing of flowering in relationship to seed size and stated that larger-seeded species flower earlier in the year than light-seeded species. In regions with seasonal climate, the limited period for plant growth (the growing season) suggests the assumption that most plant species should exhibit completed seed maturation by the end of the growing season. This trade-off tentatively suggests a positive relationship between ripening duration and seed dimension with e.g. heavier seeds requiring longer periods to produce ripe seeds. However, publications addressing the relationship between seed dimensions and the duration of the ripening process have – to my knowledge – rarely been conducted or statistically tested (but see Primack 1985). However, the ripening duration could tentatively be suggested to be somehow, indirectly or causal, linked to seed weight. Of course, the seed dimension is a crucial component of a plant species' ecological strategy (Jia et al. 2011) and directly affects pivotal life-cycle events such as establishment (Jakobsson & Eriksson 2000), competitive ability, recruitment success (e.g. Jakobsson & Eriksson 2000), and seed dispersal (Leishman et al. 2000). From a phenological point of view, the relationship between the seed ripening duration and temperature demands has been analysed for single species like *Sambucus nigra* L. and *Aesculus hippocastanum* L. (Menzel 2003). Likewise, especially for economically used plant species, models have been developed to estimate the time of seed maturity in crops (e.g. winter cereal crops; Wheeler et al. 1996; Izquierdo et al. 2013) or forest trees (e.g. Schaber & Badeck 2003). To conclude, for single species, models have already been developed to predict the timing of maturity i.e. the process of seed ripening. However, the biological importance of timing of seed ripening together with the scarceness of scientific approaches addressing related questions calls the need for studies that focus on this topic.

Within the framework of this thesis, we aimed to provide insights into the ecological and evolutionary constraints that shape late phenological phases in plants. We conducted a phenological monitoring and asked whether ecological or phylogenetic characteristics explain differences in the phenology of seed ripening. Based on the results from the monitoring, we aimed to make a first step in order to statistically estimate ripening phenology and its timing from the view of community wide patterns. The goal of the development of a statistical model that helps estimating the time of seed maturity for a large species set is ambitious but should be pursued in order to gain fundamental insights in its functioning and to further develop existing models of seed dispersal (e.g. the wind dispersal model PAPPUS Tackenberg 2003), offspring establishment and ripening of plant seeds. Furthermore, knowledge on timing of seed maturity would help in planning conservation and restoration programs. Such programs for plant population restoration should base on profound knowledge about timing of reproductive events in plants. In the interest of advising management activities, the timing of seed dispersal should be incorporated in assessments of e.g. timing of mowing in grasslands so that seed maturity and release is ascertained for certain plant populations of interest (e.g. Baumgärtner 2000; Masson, Robert, N. & Stucky, Jon, M. 2008; Reisch & Poschlod 2011). In invasive crop weed species such as *Ambrosia artemisiifolia* L. (suggested to cause allergy and asthma in humans), phenology is regarded as a key determinant for the species' invasive potential (Chapman et al. 2014; Leiblein-Wild & Tackenberg 2014). In order to effectively implement control measures to manage impacts of invasive species on human health and biodiversity, knowledge about the ripening and maturity phenology can depict crucial factors in e.g. planning of cutting dates in order to remove plant individuals before seed release and dispersal.

4.4.2 Phenology of seed release

The timing of species' seed release seriously affects various ecological factors and subsequent life cycle events. For example, the phenology of seed release and dispersal has crucial implications for germination and recruitment. Particularly in regions with a seasonal climate, the timing of fruiting is often correlated with climatic conditions that are favourable for offspring survival (Baskin & Baskin 2014). In temperate regions, germination during periods that are unfavourable for growth is prevented by various dormancy mechanisms (Fenner & Thompson 2005). Some species have seeds that are born dormant, some achieve dormancy during their life-cycle and some species have dormancy urged upon them (Harper 1977, Fenner & Thompson 2005). These different types are called innate, induced and enforced dormancy, respectively (Rathcke & Lacey 1985). For seeds germinating within the growing season they were dispersed in, the specific timing of seed dispersal can have direct impact on offspring survival. For example, earlier-dispersed seeds were found to germinate more likely than individuals that dispersed their seeds later in the year (Galloway & Burgess 2009).

Plant diaspores are connected with the parent plant by tissues that supply them with resources needed for growth and development. However, at some time, the diaspore and the parent plant disconnect from each other. Usually, a separation layer forms between the maternal tissue and the diaspore, providing a predetermined breaking point (Thurber et al. 2011). The threshold force that is required for abscission of the diaspore from the parent tissue thus decreases as the diaspore becomes more mature (Cousens et al. 2008). The timing of seed release and subsequent dispersal are likely to have direct effects on the availability of the dispersal agent. With respect to dispersal by water, periods with maximum stream discharge and rapidly decreasing flows facilitate seed aggradation and deposition. Such periods favouring seed deposition were reported to coincide with the timing of maximum seed release in species of the genera *Salix* (Niiyama 1990; Gage & Cooper 2005) and *Populus* (Cooper et al. 1999). Likewise, the seasonal availability of seed dispersing animals is suggested to coincide with the rate of plant species releasing their seeds. For example, strong relationships between fruiting seasonality and seasonal dynamics of temperate migratory birds were observed (Kimura et al. 2001). Seasonal matching of breeding period with fruiting seasonality was also reported for bats and suggested to promote seed dispersal distances (Estrada & Coates-Estrada 2001). Among Australian *Acacia* species, different phenological adaptations to the specific dispersal vectors can be observed: those plant species which have fruits that are dispersed by birds hold the seeds on the plant for a much prolonged period to match the availability of migratory birds, whereas those species dispersed by ants readily release their seeds to fall to the ground (O'Dowd & Gill 1986). For dispersal by wind, the specific timing of release is mainly affected by immediate short-term events that initiate the abscission of the diaspore from the parent plant. Such an immediate event can for instance be high wind speed that exceeds a certain threshold and thereby initiates the abscission of the diaspore and leads to higher dispersal distances compared to release under calm wind conditions (Greene 2005; Jongejans et al. 2007; Pazos et al. 2013). Natural selection on specific morphological structures that enhance abscission during environmental conditions favourable for wind dispersal is suggested to promote transport of the plant diaspores over longer distances. These specific favourable environmental conditions can be e.g. low air humidity (Lacey 1980;

Johansson et al. 2015), dry and turbulent weather conditions (Greene & Johnson 1992b; Jongejans et al. 2007), high wind speeds (Pazos et al. 2013) or thermal updrafts (Tackenberg et al. 2003b; Greene & Quesada 2011; Maurer et al. 2013). Synchronisation of seed release timing and favourable conditions can thus be achieved via mechanisms that release the seed during immediate short-term events that lead to e.g. longer seed dispersal distances.

In addition to the above mentioned matching of short-term events and release, a synchronisation with a specific season can lead to a significant enhancement of LDD. In regions with distinct seasons as for example habitats with a temperate climate or pronounced dry and rainy periods, the distinct seasons offer divergent climatic environments for seed transport over longer distances. The survey of published literature shows that explanations on how species' seed release timing differs between the seasons have, until now, rarely been provided for plants from regions with temperate climate. By contrast, for regions with a tropical climate, different studies provide concepts and interpretations on how seasonality of environmental conditions affects seed release patterns in plant communities. For example, differences in e.g. air humidity and precipitation between seasons are pronounced and show differential conditions for both seed release and dispersal. For such regions, periods offering low air humidity (Frankie et al. 1974; Griz & Machado 2001; Du et al. 2009) or high wind speeds (during typhoon season Hamann 2004 during dry season Wright et al. 2008) are commonly suggested to promote LDD by wind. A seasonal synchronisation of seed release with these periods that enhance LDD can be achieved by prolonged ripening durations during which the parent plants retains the seed by maintaining the connection to it and thereby prevents seed release during e.g. periods with calm winds (Hamann 2004). Further, such a prolonged ripening period can be interpreted as a mean to enhance wind dispersal by a synchronisation of the species' seed release period and the windiest season transporting (heavier) tree seeds over great distances (Hamann 2004). For a more detailed discussion on how both specific short-term as well as seasonal conditions influence seed release phenology and long-distance dispersal by wind in regions with a temperate climate, please see the introduction and discussion of project ii in section 8.2 on page 120 ff.

Taken together, the effect of seed release phenology on dispersal distances, despite its widely acknowledged importance, has only rarely been investigated in regions affected by seasonality such as temperate habitats (e.g. Nathan & Katul 2005; Wright et al. 2008). Thus, for temperate habitats, evidence for a synchronisation of seed abscission with periods offering favourable conditions for the ecologically highly relevant LDD is scarce. For example, for species from temperate habitats, this lack of knowledge raises the question whether wind-dispersed plant species show seasonal synchronisation of seed release with wind conditions that promote LDD by wind.

4.4.3 Phenology and its role for evolution of LDD

Rare LDD events are typically driven by large animals with widespread home ranges, migratory animals (e.g. migratory birds), extreme meteorological weather conditions, ocean currents and transport by humans (Nathan et al. 2008). LDD of plant seeds are vitally important for the spatiotemporal dynamics of species and largely impact the spread rate of plants (Clark 1998; Higgins et al. 2003a). Rare LDD events determine large-scale phenomena such as migration of plants and range shifts in order to track suitable conditions in face of climate change. Thus, despite immense difficulty in measurement and estimation, the interest in LDD research is currently increasing (Nathan 2005), particularly in plant ecology (Jordano et al. 2007).

Due to the rarity of events, LDD has often been considered as a process that is difficult to estimate and hard to understand (Higgins et al. 2003b). In fact, the idiosyncrasy of LDD, with its unpredictable occurrence (Nathan et al. 2001), has led to the traditional view of LDD as a phenomenon that may only be weakly be affected by natural selection (Berg 1983). In the search of traits that could be affected by natural selection, the dispersal processes suggested by seed morphology were, to some extent, suggested to be only loosely correlated with LDD (Higgins et al. 2003b). In other words, due to the random and accidental nature of LDD, Higgins et al. (2003b) it is questioned whether morphological traits, e.g. wing-shaped seed appendages that increase the wind dispersal potential of the diaspore, can effectively enhance rare LDD events. This suggestion, of course, caused controversial discussion about the evolutionary mechanisms that underlie LDD. Due to this ‘fuzzy’ nature of LDD, many researchers believe, that – if at all – evolution can hardly shape plant LDD. In this current debate about the heredity of traits related to LDD, the idea that LDD could evolve through changes in ‘unusual’ traits like the phenology of seed release rather classically studied morphological traits have recently been challenged (Nathan et al. 2008). Following Nathan et al. (2008), natural selection on the phenology of seed ripening and release could be a successful mean in terms of achieving higher dispersal distances. Hence, the ecological importance of the phenology of ripening and release is suggested to be underestimated or disregarded compared to more obvious LDD traits as for instance selection on morphological traits (e.g. seed surface structure or seed releasing height).

4.5 Scope of this thesis

With the research projects included in this thesis, I link fundamental knowledge about the phenology of seed ripening (project i, section 8.1 on page 76 ff.) with factors that drive both processes of seed release (project ii, section 8.2 on page 120 ff.) and seed dispersal of plants (project iii, section 8.3 on page 154 ff.). Specifically, this thesis comprises three research projects:

i. The process of seed ripening and how it is influences by species' ecology and evolution
ii. Seasonal synchronisation of seed release with long-distance seed dispersal by wind
iii. Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed

The first project mainly approaches the ecology of timing of and temperature demands for seed ripening and release. The second project covers the topic of seasonal seed release timing and examines whether it is adapted to achieve high spread rates trough wind dispersal. The third project closely examines seed dispersal by wind and how it is affected by different plant traits, meteorological circumstances and distinct landscape features. The three research projects approach different experimental set-ups. For example, project i focuses on species with different dispersal modes including dispersal by wind and dispersal by animals. In the projects ii and iii, which are both based on results from LDD simulations, mainly species that are likely to be dispersed by wind were included. For a first overview of the main characteristics of the three different research projects please see Table 1 on page 39.

Table 1: Overview about the three research projects included in this thesis.

	Project i (Ripening)	**Project ii (Synchronisation)**	**Project iii (LDD)**
Data			
Empirical data from dispersal simulations		x	x
Empirical data from monitoring	x		
Additional data from literature		x	
Number of years of empirical data	2	3	2
Species			
Type of species: Natural species	x	x	
Type of species: Model species		x	x
Vegetation type: Open habitats	x	x	x
Vegetation type: Forested habitats	x	x	x
No. of species	104	165	36
Dispersal type: Anemochory	x	x	x
Dispersal type: Epizoochory	x		
Dispersal type: Endozoochory	x		

4.5.1 Project i: How are late phenologies in plants affected by species' ecology and evolution?

In project i, we aim to gain insights into the ecological and phylogenetic constraints that affect late phenologies in plants. Specifically we raise the question: what determines the duration or energy input that is needed for seed maturation? Is it the species' phylogeny, or do e.g. morphological plant traits like the seed weight functionally shape the ripening phenology? We studied the phenology of late phenological phases, seed ripening and seed dispersal and how these are determined and shaped by plant traits and phenology. Understanding these issues is vitally important to estimate the timing of maturation and initiation of subsequent phases such as seed release and dispersal of diaspores. Previous studies on timing of ripening followed rather deterministic approaches by simply naming the periods of seed maturity and were, if at all, only available for few plant species. Knowledge about the mechanisms that shape temporal aspects related to ripening would allow projecting species' seed maturation timing and thereby enable improvement of existing seed dispersal models. Furthermore, in a more practical field of plant ecology, knowledge of seed ripening times could markedly help planning practical work in landscape management or conservation of plant populations.

In order to gain insights into the ecological and evolutionary processes that shape the phenology of seed ripening and release, we conducted a phenological monitoring of the ripening and dispersal phenology of 104 Central European plant species. This monitoring was conducted on the basic unit of flowering phenology (the single flower) in order to impede unintended effects of other factors such as population size, environmental heterogeneity, and temporal variability on the observed phenological processes. Further, an additional monitoring on 18 species in two successive growing seasons 2009 & 2010 at three locations along an elevational gradient was carried out in order to evaluate the data with respect to phenological variability within the studied species. We developed a statistical model for the relationship between ecological traits, plant phylogeny and the ripening process. We studied the temperature demands for seed ripening and hypothesised that:

H1 The temperature demands for ripening differ between ecological life forms (e.g. herbs, grasses and shrubs)

H2 The temperature demands for ripening are affected by the plant phylogeny and, for example, differ between plant families

H3 The seed weight affects the species' temperature demand for ripening.

H4 Temperature demands for ripening are species-specific and do not differ between locations at different altitudes

H5 The durations of diaspore release differ between the species' dispersal type (anemochorous, epi-, and endo-zoochorous).

In comparison to the manuscript presented in project i, here I appended the hypothesis 'H4'. By comprising this hypothesis, I deepen the discussion of results from project i that addressed intra-specific variability of temperature demands for seed ripening along an elevation gradient.

4.5.2 Project ii: Seasonal synchronisation of seed release phenology promotes long-distance seed dispersal by wind for tree species with medium wind dispersal potential

In project ii, we investigated the extent of seasonal synchronisation of seed release and favourable wind conditions as a measure for the existence of phenological adaptations of plant species to promote LDD by wind. As wind is an important dispersal vector for many plant species, it can be assumed that wind-dispersed species show a (seasonal) synchronisation between seed release timing and wind conditions promoting LDD potential by wind. In project ii, we asked whether the wind conditions that drive dispersal of seeds differ between seasons and whether natural selection on seasonal timing of seed abscission could have shaped species' seed release phenology. Further we seek to contribute to the scientific debate on the relative importance of seed release phenology vs. more classical traits like seed morphology for LDD by wind. We combined empirical observations of seed release phenology with simulations of LDD by wind. We simulated LDD by wind for 125 species from open and 40 species from forested habitats. In order to investigate the extent of seasonal synchronisation of seed release with LDD, we compared species' LDD throughout the year with phenological data on timing of seed release for herbaceous species from open and tree species from forested habitats.

Specifically, in project ii we raised the following questions:

H6 Do wind-dispersed species show a seasonal synchronisation between the timing of seed release and favourable conditions for LDD by wind?

H7 When do wind-dispersed plant species from different vegetation types release their seeds?

H8 Which species show higher potential for LDD by wind?

H9 Which are the specific wind conditions that promote species' LDD in different vegetation types and seasons?

Please note: LDD is commonly suggested to be more much higher above the vegetation cover (e.g. forest canopy) than within the vegetation. Thus, we focused our LDD simulations for project ii and iii on LDD above the closed vegetation cover in order to comprehensively compare the different habitat types.

4.5.3 Project iii: Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed

Seed dispersal by wind is strongly affected by various factors such as plant and seed traits, temporal variability, the specific landscape structure and the prevailing meteorological conditions. However, the specific roles of the mentioned factors, as well as their interactions, are still not fully understood and under lively debate in ecological research. With respect to published articles considering plant dispersal by wind, the mentioned factors were only seldom addressed in a single study and could therefore hardly be differentiated. In project iii, we simulated LDD by wind for 36 virtual model species in order to disentangle the effects of species, habitat types and meteorological conditions. We conducted an extensive wind dispersal simulation analysis and designed a dataset that was directly comparable between different vegetation types, sites and years. We generated different datasets to obtain comparability between the observed factors and parameters. Using these specifically designed datasets for different factors, we particularly studied the effects and interactions of species traits, habitat type (open vs. forested habitats), between-site differences, between-year variation and meteorological conditions on LDD by wind.

In project iii, we addressed the following questions:

H10 Does the LDD potential differ between vegetation types?

H11 Does the effect of seed terminal velocity and height of seed release on LDD differ between vegetation types?

H12 Does LDD differ between years?

H13 How do the effects of vertical turbulence, wind speed, vegetation type, seed terminal velocity and height of seed release interact?

5 Summary of the main results

5.1 Project i: How are late phenologies in plants affected by species' ecology and evolution?

We found that the temperature demands for seed ripening differed considerably between therophytes, herbaceous plants and shrubs (H1). With respect to the evolutionary relatedness of species, we found phylogenetic signals for diaspore weight, temperature demands for diaspore ripening, and timing of release (H2). The built model also showed that the diaspore weight is very important for determining the ripening process and its duration (H3). With a view to the hypotheses proposed in section 4.5, the hypotheses H1, H2 and H3 could all be verified. With respect to within-species differences in temperature demands for ripening, the monitoring along an elevational gradient (H4) showed that individuals from higher altitudes have lower temperature demands for ripening than species from lower altitudes. Hence, these differences in temperature demands between plant populations suggest that within species, temperature demands are somehow lesser strong conserved than we assumed. With a view to environmental conditions during dispersal (H5), we found low air humidity and higher temperatures during periods of seed release for light seeded herbaceous species (mainly from the Asteraceae family) with clear adaptations to wind dispersal.

5.2 Project ii: Seasonal synchronisation of seed release phenology promotes long-distance seed dispersal by wind for tree species with medium wind dispersal potential

We found a high extent of seasonal synchronization of LDD by wind with periods showing favourable conditions for wind dispersal for tree species with medium wind dispersal potential (H6; e.g. *Acer platanoides* L., *Tilia cordata* Mill.). These tree species showed an extended ripening duration and released their seeds predominantly during winter (H7). During wintertime exhibiting high wind speed periods, these species showed the highest rate of LDD by wind. Species with high wind dispersal potential from open habitats (mainly species from the Asteraceae family with plumed seeds) and forested habitats (e.g. tree species of the genera *Populus*, *Salix*) showed high LDD by wind throughout the year (H7). In open habitats, high LDD by wind was found for species with high wind dispersal potential whereas dispersal rates of species with medium or low wind dispersal potential were very low (H8). In forested habitats, species with both, high and medium wind dispersal potential showed high LDD by wind. With a view to the wind conditions that promote LDD by wind we found diverging results for the different vegetation types: In open habitats, species LDD was mainly driven by thermal updrafts (H9). By contrast, in forested habitats, LDD by wind was promoted by both, thermal updrafts and horizontal wind speed.

5.3 Project iii: Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed

We found that LDD by wind was higher in forested habitats compared to open habitats (H10). The seed terminal velocity had an effect on LDD in both habitat types, while the effect of seed release height above the canopy was only significant in open habitats (H11). In forested habitats, between-year variation in LDD was greater than in open habitats (H12). We found considerable differences in how vertical turbulence and horizontal wind speed affected LDD between species and habitat types: in general, vertical turbulence (i.e. thermal updrafts) had a great effect on species' LDD. Interestingly, we found differences between habitat types in how updrafts affected species' LDD. We found that LDD by wind of high wind dispersal potential species from open habitats is likely to be driven by updrafts (H13; e.g. species with plumed seeds). By contrast, horizontal wind speed showed a positive effect on LDD for low wind dispersal potential species from open habitats. For tree species from forested habitats with intermediate wind dispersal potential, LDD was clearly promoted by updrafts. For low wind dispersal potential tree species from forested habitats, horizontal wind speed showed a clear effect on LDD. Likewise, in open habitats the positive effect of wind speed on LDD increased with decreasing wind dispersal potential.

6 General discussion

6.1 General discussion of the main results

In this thesis, I studied late phenological phases and focused on three important processes involved in plant reproduction, namely seed ripening (project i), seed release (project ii) and seed dispersal (project iii). In the following, interpretations that were drawn from the main results (chapter 5) shall be outlined before these will subsequently discussed comprehensively.

The analyses carried out for project i indicated that the species' seed weight and the temperature demands for diaspore ripening are affected by the plant life form (H1) and by phylogeny (H2). Further, our results showed that the temperature demands for timing of release are affected by phylogeny (H2). From a more physiological point of view, the species' seed weight (H3) showed a positive relationship with the temperature demands for seed ripening. This functional relationship was largely affected by the incorporation of the three different life forms in the model. The above mentioned phylogenetic signals strongly indicate that the evolutionary history of the species' lineage shapes its diaspore weight and, as a consequence of the positive effect of seed weight on ripening demands for ripening, the ripening and seed release phenology. The results obtained from the monitoring along an elevational gradient showed that temperature demands between plant populations differed. This result of lower temperature demands for ripening of plant individuals occurring at higher elevations tentatively indicates the existence of physiological adaptations towards less temperature input for seed ripening under conditions of a shortened growing season (H4). The finding of low air humidity and higher ambient temperatures during seed release of wind dispersed herbaceous species, which was observed in project i, could be interpreted as a phenological adaptation to match favourable conditions for dispersal and to enhance dispersal distances (H5). With the models in this project, we contribute to the understanding of ecological and environmental factors that determine species' late phenologies and introduce data that that are well suitable for parametrization and further development of plant dispersal models.

In project ii, we suggest that for tree species with medium wind dispersal potential, the high extent of seasonal synchronisation of seed release timing with stormy periods during wintertime (H6) could be evidence for the existence of phenological adaptations in order to match favourable conditions during seed release (H7). From an evolutionary point of view, natural selection on the timing of seed release of both ecologically and economically important species (including species from the genera *Abies, Acer, Fraxinus, Larix*) might have belayed periods of seed release in order to match stormy wintertime. For species with high wind dispersal potential (e.g. open landscape species from the Asteraceae family or species from forested habitats including the genera *Populus* and *Salix;* H8*)*, the results suggest that uplifting of seeds is considerable and allows high LDD in each month of the year (H9). The finding that these species with high wind dispersal potential did not show a pronounced seasonal synchronisation of LDD by wind with periods showing favourable conditions for wind dispersal (H6) could possibly be due to synchronisation with weather events on much shorter temporal scales such as short time events with e.g. low air humidity. To my knowledge, the study conducted in project ii is the first that comprehensively addresses the relationship between seasonal seed release timing and LDD by wind for different vegetation types and many plant species in Central Europe. The outcomes for the role of phenology in shaping LDD display that future work in LDD research should devote increased attention to the evolutionary basis of LDD.

The results obtained from project iii generally suggest that the effects of vertical turbulence and wind speed on LDD by wind diverge for species with different functional traits (H13) as well as in different vegetation types (H11). In open habitats, the seed release height showed a clear effect on LDD, whereby in forested habitats no such effect was found (H11). For example, we found that LDD by wind of species from open habitats with high wind dispersal potential is likely to be driven by updrafts (H13, see section 5.3). From our findings in project iii, we suggest that open and forested habitats differ with respect to the relative distribution of turbulence and its resident time above the vegetation cover. Updrafts, which are mainly driven by sun that is providing energy to a surface, generally tend to generate feeble eddies that provide lift for longer and continuous periods. Above most open landscapes, we suggest that more thermally driven (weak) buoyant eddies, providing lift for longer periods, are generated (Finnigan & Kaimal 1994). Here, species with high wind dispersal potential are suggested to show promoted LDD as their seeds are light enough to be transported by the weak buoyant eddies. By contrast, shear driven turbulence, which can be driven by strong winds, is suggested to be both stronger than updrafts but also more intermittent. Above most forest canopies, thermally driven turbulence may be weaker because leaf area is large and more of the solar energy is converted to fluxes of water vapor rather than thermal updrafts. The observed strong LDD-promoting turbulences above forested habitats are, particularly for broad-leaved forest types, likely to be mainly driven by strong storms.

Hence, we suggest that strong storms produce shear-driven turbulence above forest canopies and promote LDD of species with lower wind dispersal potential (e.g. heavier-seeded tree species).

Our results from project ii and iii show considerable differences in how updrafts and horizontal wind speed affected LDD between different species and habitat types. Until now, such differences have rarely been indicated and have often been attributed to differences in e.g. model performance or study design. By basing the analyses on a broad data set that included a wide range of species traits, different vegetation types and sites, the results obtained from project iii offer answers for debates concerning e.g. the role of specific meteorological conditions enhancing species' LDD by wind. The study in project iii provides both valuable and reliable results in the field of LDD research. In LDD research that focuses on wind as a dispersal agent, seasonal variability within and temporal variability across years have only been addressed in few studies (Gomez-Aparicio et al. 2007). Here, project ii and iii provide detailed insights in temporal patterns of LDD for plant species with divergent wind dispersal potential from different vegetation types.

In the following, I concertedly discuss the relation of the three phenological phases ripening, seed release and seed dispersal to the different research questions approached in the single studies. I herewith interconnect the single research projects and will, where applicable, highlight hypothesis posed in section 4.5. I discuss the obtained findings from different viewpoints including environmental conditions, species phylogeny. Subsequently, I discuss methodological aspects of the different approaches applied in the projects and provide suggestions for prospective experimental designs that build on this thesis. Lastly, I link my results to other results on (future) climate change obtained from literature in order to broaden the discussion and provide tentative assessments of my results at a higher ecosystem level.

6.2 How do environmental conditions affect late phenologies ripening, release and dispersal?

6.2.1 Seed ripening phenology

In general, environmental conditions clearly affected the late phenologies studied in this thesis. In particular, the species' temperature demand for ripening was clearly and positively correlated with the seed weight of the species (project i). As such, heavy seeded species showed higher temperature demands for ripening than light seeded plant species. Temperature is commonly suggested as the main factor affecting plant physiology (see e.g. Larcher 2003; Badeck et al. 2004; Defila & Clot 2005). However, for late phenological phases, a weaker relationship between temperature and timing of its occurrence than for early phases such as flowering is suggested (Defila & Clot 2005). This is mainly due to the fact that in autumn factors such as for instance dry periods play a bigger role for timing of events than air temperature (Defila & Clot 2005).

In an auxiliary monitoring within project i, temperature demands for ripening were, for a smaller species set, studied along an elevational gradient. According to the results for temperature demands between different sites and along this elevational gradient, plant individuals from higher elevations (with lower mean air temperature; height above mean sea level = 690 m; Vogelsberg Mountains, Hesse) showed lower temperature demands for seed ripening than plant species from lowland elevations (height above mean sea level = 110 m; Frankfurt, Hesse). The results of significant differences between plant populations suggest that these differences might be due to selection on physiological traits that alter the temperature demands needed for seed production. Hence, local adaptation of plants to site-specific climatic conditions could explain the obtained results of differences in temperature demands for seed ripening between sites with divergent elevation. The geographically distinct populations studied may thus be genetically differentiated in the physiological demands for temperature. Local adaptations of species to climate were for example found in the herbaceous *Viola reichenbachiana* Boreau and *Aesculus hippocastanum* L. (Tryjanowski et al. 2006). By contrast, by comparing response rates of flowering onset to variations in temperature between the first and the second half of the 20th century, Menzel et al. (2005) did not find any indications for adaptation processes in *Aesculus hippocastanum* L., *Syringa* *vulgaris* L. and *Ribes rubrum* L. The assumed species' potential for adaptation to lower temperature demands for seed ripening at high elevation raises the question how these lower temperature demands for seed ripening could have emerged by natural selection. Both could be suggested that the lower temperature demands are mainly due to changes in seed size (because of the functional relationship between seed size and temperature demands for seed ripening) or alternatively that it is due to changes in the chemical composition of produced seeds (Lambers et al. 2008).

Altitudinal gradients are very powerful 'natural experiments' for testing ecological responses to geophysical influences, such as low temperature (Körner 2007). However, there are two types of environmental changes with increases of altitude: first, the changes that are tied to meters above sea level such as temperature or atmospheric pressure. Second, there are changes with increases in altitude that are not altitude-specific such as e.g. moisture, hours of sunshine and wind (Körner 2007). In fact, the Vogelsberg sites at higher elevation showed lower temperatures (following Körner (2007) 'altitude specific') and both: higher humidity and precipitation (not generally altitude specific). Thus, some gradients of environmental characteristics that affect the plant phenology are likely to interact with each other with increasing altitude (e.g. increase of relative humidity that comes along with a decrease of temperature). Thus, multiple environmental effects likely impede the explanation of differences found in the field. In addition, for wind-dispersed plants, humidity plays a considerable role for the timing of abscission (Greene & Johnson 1992b; Jongejans et al. 2007). However, in order to evaluate environmental differences in other variables than those studied in our approach, factors like sun shine duration, which is supposed to be not primarily altitude specific, should also be addressed while assessing species phenology along elevational gradients (Körner 2007). Assuming that sunshine duration rather than temperature might explain species' phenological development, the sunshine duration should be higher at higher altitudes in order to better explain the obtained results. However, with a view to differences in sunshine duration along the elevational gradient, the mean of daily sum of sunshine duration in 2009 was higher at the low elevation site 'Frankfurt' (4.78 h sunshine per day, (Deutscher Wetterdienst (DWD) 2014), data not shown in project i) compared to the site at higher elevation 'Vogelsberg Mountains' (4.14 h sunshine per day). These differences in sunshine period between the sites indicate that sunshine duration might be lesser strong related to development than temperature and strengthen the assumption that adaptations to lower temperature demands between species might have evolved in individuals occurring at higher elevations.

6.2.2 How much does the phenology of seed release and dispersal contribute to species' LDD?

Although often considered as an important plant trait that could actually underlie evolutionary selection and considerably enhance LDD of plant species, the phenology of seed release and dispersal has only rarely been studied until now. As introduced before, the role of phenology in evolution of LDD has been advanced by e.g. Nathan et al. (2008). The seed release timing of species was studied in both projects i and ii. The studies in project i and ii were carried out on different temporal scales (temporal resolution of two weeks and four weeks, for project i monitoring and project ii literature data, respectivley) and with divergent observational objects (single flower vs. whole plant communities) which shall be compared and discussed in the following. In project i we found that for anemochorous species air humidity during seed release was considerably lower than air humidity during seed release of species with e.g. primarily epizoochorous seeds. This is in accordance with findings indicating preferential diaspore abscission during periods with low air humidity in Asteraceae species (Jongejans et al. 2007) and in the moss *Brachythecium rutabulum* (Hedw.) Bruch, Schimp. & W. Gümbel (Johansson et al. 2015). The basis of selection on timing of seed release seems to be different between species with divergent adaptations to wind dispersal. According to our results obtained in project ii, timing of seed release can considerably enhance LDD by wind e.g. through preferential abscission of seeds during periods with high wind speeds. Particularly for species with medium wind dispersal potential, our results show that seasonal selection on seed release timing is likely to enhance LDD by wind. A long term (seasonal) synchronisation of species e.g. can be achieved through extended ripening periods that were found for the mentioned species group of forest species with medium potential for wind dispersal. These ripening periods can be interpreted as extended because they are much longer than ripening periods of species with similar seed weight (project ii). By contrast, for other species groups that have a higher potential for LDD by wind, our results from project i suggest that other traits than seasonality of release are shaped by selection. Here, synchronisation of seed release with low humidity has been observed at shorter temporal scales in project i. For the case of forest species with medium wind dispersal potential, which showed a pronounced seasonal synchronisation in project ii, both mechanisms namely extended ripening periods and morphological mechanisms that initiate abscission, are likely to affect LDD by wind. In fact, morphological structures that lead to preferential abscission during high wind events are well known for species with both high (Greene & Quesada 2011) and medium potential for wind dispersal (Greene & Johnson 1992b).

In general, the phenology of seed release (in terms of a seasonal synchronisation) had a significant and considerable effect for fewer plant species than expected. As an interesting result, both species groups from open and forested habitats with high wind dispersal potential (low seed terminal velocity) that are likely to be dispersed by wind over longer distances did not show an indication for phenologically-driven LDD enhancement throughout the year. This is likely to be due to an aspect of temporal resolution of the observations from the study in project ii. Morphological structures for short-term synchronisation of seed release and LDD are regarded as plant-controlled mechanisms in order to promote LDD and select favourable climatic conditions for dispersal (Jongejans et al. 2007; Maurer et al. 2013; Johansson et al. 2015). This kind of short-term temporal scale was not considered in our study, as we chose the broad temporal scale of one month in order to investigate phenological processes on the seasonal scale. The only species group that showed a seasonal synchronisation of seed release with LDD were forest species with medium wind dispersal potential. For these tree species from forested habitats (e.g. species from the genera *Acer*, *Fraxinus*, *Carpinus*, *Tilia*), we found a pronounced synchronisation of seed release in autumn and winter with meteorological events promoting LDD by wind. Here, LDD in wintertime was particularly enhanced by strong winter storms with that led to strong turbulence. Our findings from project ii and iii showed that the role of high wind speed increased with decreasing wind dispersal potential (e.g. heavier seeded tree species) in both open and forested habitats. To conclude, it can be assumed that the role of seasonal LDD enhancement, which may be mediated by phenological adaptations towards seasonal synchronisation of release and favourable conditions, increase with decreasing wind dispersal potential of the species' seeds.

6.3 How much does the species' phylogeny affect plant phenology?

The outcome of the analyses from project i shed light on important traits that determine the seed ripening phenology. In project i, three effects of plant phylogeny on traits related to phenology were found. The species' relatedness had a clear effect on (a) species' seed weight. In other words, closely related species showed similar seed weight. This effect of seed weight was reflected by an effect of the plant phylogeny on (b) the ripening duration. This finding is furthermore clearly visible through the significant correlation between the species' temperature demands for seed ripening and seed weight. With heavier seeds that show greater ripening durations, the phylogenetic effect of seed weight further resumes in the effect of plant phylogeny on (c) the timing of seed release.

According to the results from project i, the strong effect of seed weight on the ripening times of plant species indicates its major role in shaping patterns and processes in plant phenology. This result is in accordance with the supposed assumptions made by Primack (1985, 1987) and contrasts with findings obtained by Eriksson & Eriksson (1997). The limited period for flowering and reproduction within a growing season together with species' ripening duration that is primarily determined by seed weight could lead to the assumption that the flowering time should follow patterns or constraints imposed by the species' seed weight. Although the species groups examined in project i showed different patterns in flowering initiation (e.g. shrub species flowering solely in April and May), the flowering time did not show a phylogenetic signal (as also found by Ollerton & Lack 1992). Hence, species' flowering times may, if at all, only partially be interpreted as a result of ripening duration.

The above mentioned effect of phylogenetic relatedness on (i) seed weight has implications for the wind dispersal potential of plant species. As stated in project iii, the species' wind dispersal potential is affected by the seed terminal velocity, which is highly affected by seed weight and by the surface structure of the diaspore (see also Greene & Johnson 1992a, 1993; Tackenberg et al. 2003a). Dependent on the amount of inter-specific differences in seed surface structure, it could tentatively be assumed that closely related species might show similar wind dispersal potentials.

Considering the finding of a clear phylogenetic signal of seed weight, ripening duration and seed release timing (project i), other examined issues like the seasonal synchronisation of seed release and favourable conditions for wind dispersal (suggested as phenological adaptations; project ii) could be interpreted in a new light. The morphological or physiological mechanisms that are likely to be involved in evolution of (phenological) adaptations towards synchronisation with favourable conditions are likely to be conserved in the species phylogeny. Examples of such adaptations are rapidly developing abscission layers (Jongejans et al. 2007), morphological mechanisms for preferential abscission during updrafts (Maurer et al. 2013) or extended ripening periods to match the seasons showing favourable wind conditions (Hamann 2004). I suggest that these adaptations could also be found among phylogenetically related species in that lineage. Phylogenetic signals of phenological adaptations seem thus, from an evolutionary point of view, likely. In general, the species that were analysed in project ii were grouped according to their seed terminal velocity and could tentatively be suggested to exhibit similar seed weight. In project ii, the particular species group that showed a clear synchronisation of seed release with favorable conditions for LDD comprised ten tree species from forested habitats with medium wind dispersal potential. Further, these species showed similar (and prolonged) ripening durations and rather late seed release timing (in wintertime). Although a closer look to the relatedness of these ten species shows a phylogenetic clustering (with three species from the order Sapindales and two conifer gymnosperm taxa from the order Pinales) the low species number in this group does not allow a reliable test for a phylogenetic signal (Kembel et al. 2010).

6.4 Methodological aspects

6.4.1 Choosing temporal and spatial resolutions of phenological observations

Temporal resolution of phenological observations

In this thesis, I link studies with diverging methodological approaches and data sources ranging from phenological monitoring to ecological modelling. While both projects i and ii address phenology (for the phases ripening and seed release) and seed release synchronisation, the underlying data originates from divergent sources: the monitoring data on ripening and release (project i) was compiled with a temporal resolution of two weeks and focussed on single flowers. By contrast, the literature data on seed release phenology (project ii) had a coarser temporal resolution of one month and was based on literature data that considered phenological data on the biological scale of the community. Even though the difference in temporal resolution between both studies was only two weeks, the results were divergent. While results from project i showed seed release synchronisation for species with high wind dispersal potential, results from project ii did not show such a synchronisation for light-seeded species. On the one hand, the project ii result of an absence of indication for synchronisation of seed release with favourable conditions for species from open and forested habitats with high wind dispersal potential (low seed terminal velocity) is likely to be due to a rather coarse temporal resolution. As earlier suggested by Greene (2005), much shorter averaging times and observational periods should be approached in order to gain more precise insights into short-term events during seed release that are highly likely to promote LDD by wind. On the other hand, the absence of a seed release synchronisation for species with high wind dispersal potential is likely to be due to the different observational object between projects i and ii. Single flowering monitoring, as carried out in project i, provide much higher accuracy and allowed an insight into short-term synchronisation for light-seeded species. However, future studies following the single-flower approach should be carried out on finer temporal scales in order to better understand short-term mechanisms that promote LDD.

In project ii, the specific role of meteorological parameters that enhance LDD by wind was assessed by comparing mean values for updrafts vs. mean values for horizontal wind speed from a seasonal perspective. Here, differences in mean values of wind parameters were compared between months that showed highest and lowest LDD. In the interest of constructing a preferably broad data basis, for project ii all available meteorological data had been considered in the analyses. By contrast in project iii, the goal was to obtain a dataset that was directly comparable between different vegetation types, sites and years. Therefore in project iii, different datasets were condensed to the obtain comparability between the observed factors and parameters. Even though the methodological approaches to investigate the role of updrafts and wind speed for LDD by wind differed between both projects, the main outcomes from project ii and project iii are congruent. This finding indicates that for this specific research field extra work of generating fully comparable data sets does not necessarily have to be carried out in order to produce comparable and reliable results.

6.4.2 Further development of the model for estimating ripening phenology

The model built in project i revealed variables that significantly drive the ripening process of plant seeds of a broad species set of Central European plant species. This model should subsequently be evaluated with respect to its accuracy of prediction and its putative transferability on other plant species. The results of the GLM analyses showed that the differences of both seed weight and the temperature demands for seed ripening were remarkably different between the three studied life forms. These differences were highly important for the overall statistical relationship (among all studied species) between seed weight and the temperature demands for seed ripening. Although all three life forms contributed to the mentioned statistical relationship, the respective species numbers per life form were quite uneven. As explained in project i, this particular study design was chosen in order to reflect the proportions of species per life form of the flora of Central Europe according to data presented in Ellenberg (1991). Hence, for therophytes and shrubs a reliable prediction of temperature demands for seed ripening is hardly possible with the few species included in the study. Subsequent versions of the model should therefore explicitly focus on comprising more species from these two life forms in order to balance the species number per life form.

Evaluation of the developed model for seed ripening

In order to apply the newly parametrised and developed model on seed ripening (project i) to estimate ripening phenology, the accuracy of model predictions should first be evaluated. Due to the above mentioned reasons of low numbers for therophyte and shrub species, further model evaluation should address the main data, i.e. data on herbaceous plant species. For testing model predictions, the original data (among others: Table i-A 7) should be used and be split in order to generate two separate data sets: (a) a training data set that is used to develop the training model and (b) a testing data set that is used to calculate the accuracy of model predictions. Thus, in a first step, the model should be set up by using a subset (e.g. 45 randomly chosen species out of the 89 herbaceous species) from the original data set. Previous analyses showed that the incorporation of all three life forms have an important effect on the statistical relationship and significance of the variables (see above) which is why these life forms should be incorporated in model development. In a second step, this newly developed model could then be used to predict temperature demands for ripening of the remaining 44 species that were not used to estimate the model. Hence, based on data that originates from the exact same methodological approach, the deviation from the temperature demands predicted by the model should illustrate how reliable the predictions are. If the difference between predicted and observed values is too big, the mentioned procedure could alternatively be carried out by randomly dividing the data in five equally-sized data sets and performing a cross-validation: the procedure mentioned above would then be repeated five times until each of the five subsets has been used as the testing data set.

Future steps in modelling ripening phenology

With the results from project i, fundamental insights were gained regarding the constraints and functional relationships in seed ripening of plants. In future studies, this understanding may be used to enhance predictions for timing of seed maturity of wild plants (as discussed in section 4.4.1). In the following, I suggest to tentatively apply the developed model to predict temperature demands for ripening of plant species that were not previously considered in the original study and to evaluate these predictions according to the above mentioned procedure. In my phenological observations, individually marked flowers were repeatedly observed and monitored for the developmental range from flowering to full seed release. To my knowledge, comparable data covering more than 100 species is not available elsewhere in literature. For modelling the species temperature demands for seed ripening, data on species ecology (seed weight, life form, and phylogeny) were, within this thesis, suggested to enable predicting the phenology of seed maturity. With trait data bases at hand (such as D^3 - Dispersal Diaspore Database: Hintze et al. 2013 or TRY Plant Trait Database: Kattge et al. 2011), data on species' flowering time, seed weight, life form and phylogeny are available and should be used in order to further develop approaches to model species' ripening phenology and to extend used models to a broader species set.

So far, only few previous studies addressed the issue that abiotic factors may limit ripening times. Here, both projects i and ii contribute to the gain of insights into the relationship between the plant life form and its seasonal and environmental limitations for phenological development and finalisation of reproduction. The results from project i were used in order to gain first insights into the processes that underlie the formation of mature plant seeds. In future scientific approaches, these results for ripening temperature demands (cumulative temperature sums) should be used to build a (statistical) model to estimate the seed ripening process of plants. They should further be used to incorporate plant traits that showed a pivotal effect on ripening (mainly seed weight, phylogeny and plant life form). In order to enhance the explanatory power of the described model, the flowering time should be included as an explanatory variable, particularly due to fact that its phenology is well known for most Central European plant species. With such a model, the consideration of seed release periods of wild plants could be estimated for plant species that were not considered in the presented study. The implementation of estimated seed ripening periods of wild plants may help to clearly further develop seed dispersal simulation software such as PAPPUS (Tackenberg 2003) or SEED (Will & Tackenberg 2008). Interestingly, for cereal crop species models that express the relationship between temperature sums above a threshold and plant growth have already successfully been fitted in *Zea mays* L. and *Triticum spec*. (e.g. Hunt et al. 2003).

6.5 Species phenology and survival under climate change

6.5.1 Future environmental change in Central Europe

As the development of plants is strongly correlated with climatic constraints (especially temperature), both past and future climate changes have direct and measurable consequences for plant phenology. For the timing of flowering it is well known, that a warmer climate enhances the timing of flowering (e.g. Menzel et al. 2006). As repeatedly illustrated in phenological literature, plants that flower in spring are commonly suggested to be most sensitive to warming (e.g. Fitter & Fitter 2002). Climatic effects on late phases are rarely studied (Sparks & Menzel 2002) and can therefore hardly be estimated under future conditions.

In general, the global temperature is seriously affected by climate change with a (gradual) overall increase. Human-induced climate change is detectable within the period of the past 100 years and is even predicted to enhance in the next century. According to the Intergovernmental Panel on Climate Change (IPCC), global mean surface temperature has increased by 0.7 °C over the last 100 years. In the period between 1990 and 2005 an (gradual) increase of the global average temperature of 0.2 °C per decade was observed (IPCC 2007). The global increase in temperature is unequally distributed across the globe: annual mean temperatures in Europe are likely to increase more than the global mean (IPCC 2007). The warming in northern Europe is likely to be largest in winter and that in the Mediterranean largest in summer (IPCC 2007).

Besides such a gradual increase in temperature, extreme climate events are projected to become both more intense and frequent (Katz & Brown 1992; Beniston et al. 2007). In particular, changes in the variability of climate are suggested to affect the frequency of extreme events. Changes in the occurrence of extreme events are unequally distributed across Europe. For example, by the end of the twenty first century, regions in Central Europe are projected to experience the same number of hot days as are currently found in southern Europe (Beniston et al. 2007). Here, the intensity of extreme temperatures increases more rapidly than the intensity of moderate temperatures. With a view to changes in precipitation, Europe is projected to experience increases of the intensity of extreme events. In particular, northern regions of Europe (e.g. Scandinavia) are projected to experience a higher increase of the intensity of extreme events than southern regions of Europe (Larsen et al. 2009). Increases in heavy winter precipitation are projected for Central Europe, whereby increases in heavy summer precipitation are projected for north-eastern Europe (Beniston et al. 2007).

Induced by todays and future climate change, for many Central European plant species geographical regions offering suitable habitats experience a north-eastwards shift (Cunze et al. 2013). Predicted shifts of the geographical ranges vary (Parmesan & Yohe 2003) and are greatly challenging for plant species and their survival (Thuiller 2007). In fact, according to results of Cunze et al. (2013), many Central European plant species are expected to be limited in their dispersal potential.

6.5.2 Potential effects of future climate change on species' late phenological phases

Temperature demands for seed ripening were clearly and positively correlated with the species' seed weight. For species with higher seed weight, the ripening of seeds takes much more time and exhibits higher temperature demands than for light seeded plants. Hence, production of ripe seeds primarily depends on species-specific temperature demands for ripening. With respect to future environment conditions that are expected to show higher mean temperatures, it can be tentatively suggested that such conditions may lead to shorter seed maturation periods. Hence, absolute potential impacts of changes in temperature on timing of seed maturity are likely to differ between plant species. It is conceivable that heavy-seeded species could exhibit a considerable sensitivity to temperature changes in terms of absolute temporal shifts for seed maturation. In other words, with higher temperatures, heavy-seeded species are likely to experience earlier timing of seed maturation. From the viewpoint of intra-specific variability in temperature demands for ripening, the results from the auxiliary monitoring indicated that the species' temperature demands for ripening differ between sites with divergent temperature regimes. I interpreted these differences as adaptations towards lower temperature availability at higher altitudes. Similar local adaptations were also found by Tryjanowski et al. (2006) (see subsection 6.2.1). By contrast, no indications for adaptations processes to human-induced rapid changes in climate were previously suggested (Menzel et al. 2005). Hence, further investigations of species' temperature demands for ripening between different years (but at the same study site) seem important in order to estimate the extent of phylogenetic conservation of these phenological characteristics. However, it should be noted that the suggested pattern of reduction of periods for ripening relies on the basic assumption that production of ripe seeds primarily depends on temperature (project i). In further studies, other variables, such as the photoperiod should also be considered to gain a broader insight into other possible variables influencing seed ripening.

As introduced above, I suggest temperature increase induced shifts in ripening duration and enhancement of seed release timing to be possibly considerable for large-seeded plant species (e.g. shrubs) with higher temperature demands. Such shifts may implicate subsequent factors such as release and dispersal involved in reproductive phenology. Species with medium wind dispersal potential and medium seed weight analysed in project ii showed a pronounced effect of seasonal seed release timing on LDD by wind. These species were tree species from genera such as *Acer*, *Alnus*, *Carpinus*, *Fraxinus*, *Larix*, *Pinus*, and *Tilia* and showed a remarkable seasonal synchronisation of seed release with winter storms. The suggested reduction of ripening times raises the question, whether potential earlier completion of seed maturation may lead to a mismatch of seed release times and favourable conditions for wind dispersal. I suggest that such a mismatch is rather unlikely to negatively affect the extent of seasonal synchronisation. Even if, under future climate conditions with higher ambient temperatures, the tree diaspores should reach seed maturity earlier within the growing season, the specific timing of seed release is primarily driven by other means such as short-term events (e.g. wind gusts) causing abscission of the seed from the mother plant. In addition, ripening times of these tree species seem to be extended and remind of the prolonged ripening periods of tree species to match optimal periods for wind dispersal reported earlier (Primack 1987; Hamann 2004). During these extended ripening periods seeds are mostly ripe but are still attached to the mother plant, even if they are likely to be already fully ripe and viable. This indicates a loose relationship between ripening periods (that can be somehow prolonged) and effective seed release and emphasizes the impression that changes in the timing of seed maturity will not directly affect the timing of seed release. By contrast, for light seeded plants like species from the Asteraceae or Poaceae family that mostly have rapidly developing seeds I suggest that the effect of changes in the ripening period to be minor. For light seeded species that mainly have high wind dispersal potential, the seasonal timing of seed release seems to be less important than for species with higher seed weight. Light seeded species exhibit a “quick” response to environmental conditions. Hence, the frequency of extreme events like increases in hot days, drought, and rain fall could considerably affect their timing of seed release.

Of course, the processes that result in seed abscission differ between dispersal syndromes. For wind dispersed seeds, increases in the frequency of events with low air humidity in Central Europe could affect the timing and quantity of released seeds. Periods that exhibit low air humidity (e.g. during droughts in summer) could therefore eventually facilitate seed abscission and promote subsequent dispersal by e.g. strong and consistent thermal updrafts. By contrast, for endozoochorous plant species with fleshy fruits, the temperature demand for ripening is likely to affect the seed release phenology. As observed during monitoring of endozoochorous species, seed abscission seemed to be mainly driven by the weight of the diaspore (data not shown). For example, abscission of diaspores of e.g. *Crataegus laevigata* (Poir.) DC. initiated immediately after the ripening (estimated by color change from green to red). Thus, an effect of temperature increase on seed release of fleshy diaspores should be further studied in order to reliably estimate a potential enhancement of seed release and the interaction with seed dispersing animals.

6.5.3 Potential future conditions for wind dispersal under climate change

With respect to climate-change induced changes in the availability of wind, several models project increases in average and/or extreme wind speeds in northern and/or Central Europe (e.g. Zwiers & Viatcheslav V. Kharin 1998; Pryor et al. 2005a; Beniston et al. 2007). According to modelling of near-surface windiness in Europe, the number of future storm events is projected to increase up to 20 % (Rockel & Woth 2007). By contrast, little evidence exists for the opposite direction, in which future windiness is projected to decrease in Europe (compare Pryor et al. 2005b).

For Central Europe, both the strength of wind storms and the frequency of storm events (Knippertz et al. 2000; Beniston et al. 2007; Rockel & Woth 2007) is projected to experience increases according to various studies (e.g. Zwiers & Viatcheslav V. Kharin 1998; Pryor et al. 2005a; Beniston et al. 2007, see introduction). Precisely, climate change-induced changes in windiness over Europe are projected to differ more pronouncedly between seasons with increases in future mean daily wind speed during winter months and a decrease during autumn (Rockel & Woth 2007). This could actually have direct consequences for LDD of species. In particular, the results of (Rockel & Woth 2007) taken together with the results obtained in project ii suggest that the impact of changes in the seasonal distribution of wind conditions might be divergent for different species groups. For example, forest species with medium wind dispersal potential showed highest LDD during stormy wintertime (project ii). Hence, these species might benefit of increases in wind speed during winter time. By contrast, species from open landscapes with different wind dispersal potential were found to mainly disperse in autumn. Even though both frequency and strength of windiness are projected to increase with climate change in Europe, for many species changes in mean wind speed are not likely to considerably affect dispersal distances because they are simply not released below a certain threshold for seed abscission (Greene & Johnson 1992b; Jongejans et al. 2007). Besides changes in the intensity of wind, and in particular extreme events, the directionality of wind is projected to change in future European climate (Beniston et al. 2007). In particular, under conditions of future European climate, wind is projected to become more north-westerly than currently (Beniston et al. 2007). This could contribute to higher migration rates obtained by wind dispersal that are needed in order to cope climate change-induced range shifts projected for Central European plant species (Cunze et al. 2013).

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8 Appendix

8.1 Project i: How are ripening and seed release affected by species' ecology and evolution?

This manuscript has been submitted to a peer-reviewed journal as: Heydel, F., & Tackenberg, O. "How are ripening and seed release affected by species' ecology and evolution?"

Erklärung zu den Autorenanteilen

an dem Manuskript: How are ripening and seed release affected by species' ecology and evolution?

Status (*submitted, under review, in revision, accepted*): in revisiond

Beteiligte Autoren:

- Felix Heydel (corresponding author) (FH, Promovierender)
- Oliver Tackenberg (OT, Betreuer)

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?

(1) zu Entwicklung und Planung

Promovierender: 40%
Co-Autor OT: 60%

(2) zur Durchführung der einzelnen Untersuchungen und Experimente

Promovierender: 98% FH führte die Feldarbeit selbstständig durch
Co-Autor OT: 2% OT beriet die Feldarbeit, war bei der praktischer Durchführung nicht involviert

(3) zur Erstellung der Datensammlung und Abbildungen

Promovierender: 70% FH führte die Datenaggregierung, -aufbereitung und die Qualitätskontrolle durch. FH erstellte die Datengrundlage und Abbildungen für das oben genannte Manuskript.
Co-Autor OT: 30% OT beriet die Abläufe der oben genannten Datenarbeiten.

(4) zur Analyse und Interpretation der Daten

Promovierender: 75% FH führte die Analysen durch.
Co-Autor OT: 25% OT betreute die Durchführung der statistischen Analysen aus.

(5) zum Verfassendes Manuskripts

Promovierender: 95%
Co-Autor OT: 5%

8.1.1 Abstract

Late plant phenological phases are important for dispersal, reproductive success and survival of plants. Most phenological studies, however, consider early phases of plant development. Here, we ask how the two late phenological phases - ripening and diaspore release - are shaped by ecological and evolutionary forces. We conducted phenological monitoring of the single flower level for 104 plant species from Central Europe. Further, we undertook an associate monitoring study over two years along an elevational gradient. Data on cumulative temperature sums needed for the ripening process were related to species' data on life form, diaspore weight and phylogeny. We found that the diaspore weight of species was positively correlated with temperature demands for ripening. Shrub species showed the most efficient ratio of temperature demands for diaspore ripening and seed weight. With respect to the evolutionary relatedness of species, we found phylogenetic signals for diaspore weight, temperature demands for diaspore ripening, and the timing of release. These signals strongly indicate that the evolutionary history of the species' lineage affects its diaspore weight and, by implication, the temperature demands for diaspore ripening and the timing of release. With respect to the species' dispersal mode, anemochorous species showed higher temperature and lower relative humidity during diaspore release than epizoochorous species. For such species, the synchronisation of release timing with periods of favourable environmental conditions for wind dispersal could be interpreted as a phenological adaptation to increase dispersal distances. According to the monitoring along the elevational gradient, individuals from higher altitudes showed lower temperature demands for ripening than species from lower altitudes. This might tentatively indicate physiological adaptations to lower temperature demands for locations with a shorter growing season. Our study provides basic knowledge about factors that affect late phenological phases and facilitates the further development of models for estimating ripening phenology of plants.

8.1.2 Introduction

The phenologies of seed ripening and release are key life history traits that strongly affect the reproductive success of plant species (Rathcke and Lacey 1985). Nevertheless, only few studies on the phenology of plant species examine these late phenological phases (e.g. Rathcke and Lacey 1985; Menzel 2003). By contrast, early phenological phases such as e.g. germination of seeds or flowering are addressed in several phenological studies (e.g. Jia et al. 2011). This might be because most seeds are less conspicuous than emerging seedlings or opening flowers and late phases are often hard to define (Sparks and Menzel 2002). Hence, only little is known about the ecological factors that deter the ripening phenology of plant seeds. Taking account of the seasonality in the availability of dispersal vectors like wind and animals, insights into the phenology of ripening are crucial determinants while assessing plant species spatiotemporal dynamics. However, the biological importance of late phenological phases together with the scarceness of scientific approaches addressing related questions calls the need for studies that focus on this prominent topic in plant dispersal ecology.

In general, the phenology of plants can be studied on different observational levels. For instance, plant phenology can be studied for a whole community, a particular plant population, for the flowers of a single plant or even for an individual flower (Primack 1985). Between these observational levels, the constraints and selective forces that influence the timing and duration of different phenological phases differ (Fenner 1998). Hence, even under similar environmental and biotic conditions, phenological patterns and processes are suggested to differ between the observational levels. Considering these differences between phenological levels, many studies that aim to assess the relationship between plant phenology and plant traits comprise methodological limitations. For instance, the environmental landscape heterogeneity implicates an environmentally based variability in the phenology of plants. Changes in population size can strongly affect the onset of flowering (Miller-Rushing et al. 2008). As there is temporal and spatial variability in climate, of course, the plant phenology varies between sites (Lack 1982) and years (Horvitz and Schemske 1990; White et al. 1997; Chmielewski and Rötzer 2002). Further, on the landscape and on the population level, many factors such as size of the plant population, soil characteristics, meso- and microclimate, differently affect the plant phenology. Hence, many phenological studies are conducted on large spatial and temporal scales in order to account for the different sources of variability in phenology (meta-studies, e.g. Menzel et al. 2006). However, while aiming to assess the relationship between plant phenology and plant traits (e.g. diaspore traits), studies focusing on the basic unit of flowering phenology (the single flower) allow inference, which is not affected by other factors such as population size, environmental heterogeneity, and temporal variability. The approach of focusing on the single flower offers the opportunity to address the relationship between plant phenology without comprising the mentioned biases. However, until now, such studies have been rarely pursued.

Plant phenology and its temporal aspects are primarily driven by 'external' i.e. environmental constraints like seasonality of temperature. In most temperate species, it appears that temperature and, albeit to a lesser extent, photoperiod (i.e. day length) are the main factors that determine (vegetative) phenologies and are used to determine between seasons (Rathcke and Lacey 1985; Samach and Coupland 2000; Lambers et al. 2008). Temperature plays the role of developmental initiation in a particular way. In general, it is the sum of temperatures experienced over some period of time (cumulative temperature sum) and not the specific temperature on a particular day that determines the timing of a developmental phase (Wielgolaski 1999; Larcher 2003; Menzel et al. 2006b). In order to reduce physiological risks, plants (like many other organisms) furthermore use the day length as a reliable predictor of the average temperature and thereby e.g. avoid leaf flush in winter due to a warm spell (Gurevitch et al. 2006).

The phenology of flowering is well known to physiologically depend on a certain (minimum) availability of temperature (Larcher 2003). However, the phenology of seed ripening is widely believed to be (additively) shaped by 'internal factors' such as phylogeny (Primack 1985; Rathcke and Lacey 1985; Larcher 2003). Evidence for phylogenetic conservatism in phenology is provided by Kochmer and Handel (1986) who found that the phylogenetic membership strongly influences the species' flowering phenology. The flowering phenology is, albeit to a lesser degree, also constrained by the life form of species (e.g. trees vs. shrubs vs. annuals) Kochmer and Handel (1986). With respect to seed characteristics, species-specific plant traits like seed size and volume probably fix the ripening duration of seeds (Primack 1985). With a given species-specific ripening duration, a developmental correlation between the timing of seed maturation and the timing of flowering is suggested (Primack 1985). Hence, the timing of flowering could be an outcome of selection for the timing of seed ripening. For example, Jia et al. (2011) found evidence for a positive relationship between seed weight and timing of flowering. In general, seed characteristics may represent a major factor controlling the process of ripening and the timing of flowering and are both probably conserved in the species phylogeny (Davies et al. 2013). By contrast, the duration of diaspore release is often suggested to be an outcome of a synchronisation of the event of seed abscission with periods favouring the respective dispersal vector (e.g. Heydel et al. 2015). In wind-dispersed species, for example, such a synchronisation can be achieved by means of morphological structures for preferential abscission during short-time events like e.g. low air humidity, high wind speed (Pazos et al. 2013) or thermal updrafts (Maurer et al. 2013) and thereby lead to dispersal of seeds over greater distances. For animal-dispersed plant species with fleshy fruits (e.g. shrubs), temporal aspects of diaspore release are often phenologically adapted to the availability of dispersing animals (e.g. Herrera 1984; Griz and Machado 2001; Du et al. 2009).

Because of the mentioned differences in the phenology of diaspore release, it can be assumed that the duration of diaspore release differs between species with different dispersal modes of species. Most of the mentioned examples assessing the nature of differential factors shaping the process of seed ripening and the duration of diaspore release concern the phenology of trees. However, for herbaceous plant species empirical evidence is scarce.

To provide more insights into the ecological and evolutionary constraints that shape the species' late phenological phases of plant reproduction, we conducted a phenological monitoring on the single flower level for 104 plant species and asked whether ecological or phylogenetic characteristics explain differences in the phenology of seed ripening and release. We studied the temperature demands for seed ripening and hypothesise that (i) the temperature demands for ripening differ between ecological life forms (e.g. herbs, grasses and shrubs), that (ii) the temperature demands for ripening are affected by the plant phylogeny (e.g. between plant families), (iii) seed weight affects the temperature demands for ripening, and that (iv) the duration of diaspore release differs between the species' dispersal type.

8.1.3 Material and methods

8.1.3.1 Phenological monitoring

In order to investigate the role of both plant traits and phylogeny for the process of ripening, we conducted a phenological monitoring for a broad species set of 104 plant species from different plant families and plant life forms from Central Europe. The main phenological monitoring was accomplished in the year 2009 in the Botanical Garden of the Goethe University Frankfurt, Germany. In order to assess the effect of location and different growing seasons on the phenology of species, we conducted an 'associated monitoring' for 18 species in two years (2009 and 2010) at three different locations along an elevational gradient. The locations were (i) the Botanical Garden of the Goethe University Frankfurt, (ii) Lower Vogelsberg Mts., and (iii) Higher Vogelsberg Mts. (all located in Hesse, Germany: see Table i-A 1 on page 102 for details of site characteristics).

For the phenological monitoring, five intact individuals were chosen for each plant species. During the peak of the species' flowering period, five vital individuals that initially began to flower (most flowers still closed) were chosen for marking of flowers. For each individual plant individual, five single flowers were individually marked using coloured strings. Thus, for each species 25 flowers were examined regarding their developmental phase in a biweekly interval in all three study areas. In order to account for different durations of plants within the different phenological stages, we applied an adjusted phenological monitoring that was based on the scale of the 'Biologische Bundesanstalt, Bundessortenamt and Chemical industry' (BBCH) Meier (1997) and comprised nineteen developmental stages (Table i-A 2). The monitoring data of each single flower were quality assured after the following procedure. Flowers were incorporated for further analyses for the case that phenological observations in both phases flowering and diaspore release were made. Phenological monitoring data was also checked with respect to inconsistency in phenological recordings. Flowers were discarded from the analysis if recorded stages showed a shift from diaspore release back to flowering or a shift from ripening back to flowering. For each species, a minimum of 16 individually marked flowers were comprised in the analyses (mean number of flowers per species was 34, see Table i-A 3). The durations of flowering, ripening, and release were calculated as the difference between the last and first date of the respective phase.

8.1.3.2 Climatic parameters and calculation of temperature demands for duration of phenological phases

Climatic data for the study sites was obtained from German Meteorological Service for three weather stations adjacent to the study sites (Table i-A 1, Stationsnetz Deutscher Wetterdienst, (Deutscher Wetterdienst, DWD 2014). Data on temperature and relative humidity were calculated as a daily average and precipitation was calculates as the daily sum.

In temperate regions, many phenological phases as for example flowering and onset of ripening are well known to be physiologically depend on a (minimum) availability of temperature (Larcher 2003). For each species, we calculated the cumulative temperature sums from 1 January (Hunter and Lechowicz 1992) to mean date of both flowering and diaspore release. In contrast to most methodological approaches in phenology research, we focused rather on the duration and temperature demands of phenological phases. Hence, we calculated the cumulative temperature sums during the periods of ongoing flowering, ripening and diaspore release. In the mentioned analyses, cumulative temperature sums were calculated of daily mean temperatures that exceeded 5 °C.

In order to assess differences in environmental conditions during the periods of diaspore release between the dispersal modes, we calculated mean temperature, humidity, and precipitation during the period of ongoing diaspore release, for each single flower. For the analyses, mean value of the respective environmental variable were calculated for each species separately.

8.1.3.3 Data on ecological traits of the species

The studied species were classified in in three different life forms: ‘herbaceous’ plants (including herbaceous chamaephytes, hemicryptophytes, and geophytes), therophytes and nanophanerophytes (shrubs) according to data presented in Ellenberg (1991). The dispersal mode of the species was classified according to diaspore trait data obtained from Hintze et al. (2013). Species with a low seed terminal velocity (most species with seed terminal velocity < 2 ms^{-1}) or diaspores with apparent wings were classified as ‘anemochorous’. Species that produce seeds with appendages (or a mucilaginous surface) and seed terminal velocity greater than 2 ms^{-1} were classified as ‘epizoochorous’ (see. Table i-A 4). Species with nutrient rich seeds or appendages were classified as endozoochorous. If the dispersal mode could not be assigned unambiguously, the dispersal mode of a species was classified as ‘unspecialised’. The number of studied species per dispersal mode and life form is provided in Table i-A 5.

8.1.3.4 Measurements of weight of morphological structures related to ripening and dispersal

In order to examine the effect of the weight of morphological structures on seed ripening and release, we differentiated the species' germinule, diaspore and, if present, the flower head (including vegetative structures and seed material). For each morphological structure, we measured the weight of at least ten objects (except a few flower heads, see Table i-A 3) and calculate the respective average values. The weight of lightweight structures (weight < 14 mg) was measured using an electronic microbalance of the series 4401 MP8 (company Sartorius Mechatronics, Göttingen, Germany). For structures with a weight > 14 mg, CPA Analytical Balance CPA225D was used. We calculated the species-specific ripening quotient as a relative measure for the 'efficiency' of the ripening process. We divided cumulative temperature sums for ripening by both species' weight of germinule and weight of diaspore, separately. Hence, assuming e.g. similar diaspore weight of two different life forms, a low ripening quotient indicates a more efficient ripening process.

8.1.3.5 Data analysis

To test the effect of life form and weight of different morphological structures on temperature demands for ripening, a linear model (LM) was set up with the dependent variable 'temperature sum for ripening' and the explanatory variables 'life form', 'weight of the germinule (i)', 'weight of diaspore (ii)' and 'weight of the entire flower head (iii)'. Three LMs were set up to test for between-dispersal mode differences in (i) 'temperature sum for ripening', (ii) 'temperature sum for diaspore release', (iii) 'duration (days) of diaspore release'. We used a LM to test for differences in seed weight between the plant life forms. Using a GLM of the Gamma error distribution family, we tested for differences in the ripening 'efficiency' between life forms. LMs and GLMs were set simplified using backward selection of the non-significant variables until the final minimal adequate model contained only significant terms (p value <0.05, Crawley 2007) and a minimal Akaike Information Criterion (AIC) was obtained (Crawley 2007).

We used the data set from the 'associate monitoring' (see section Phenological monitoring) to test for the effect of 'year' and 'site' on 'temperature sum for ripening'. Differences in the environmental variables (i) temperature, (ii) relative air humidity, and (iii) precipitation between the three sites were analysed using environmental data from years 2009 and 2010 (see methods section ‘Climatic parameters and calculation of temperature demands for duration of phenological phases’).

In order to generate a measure of the degree to which phylogeny predicts phenological similarity between species (Blomberg et al. 2003), we tested for a phylogenetic signal of the traits temperature demands for flowering, ripening and diaspore release and mean date of flowering and diaspore release by using the function ‘multiPhylosignal’ (R package ‘picante’, with 10 000 replications, Kembel et al. 2010). Data on phylogenetic relationships between the studied species was obtained from (Durka and Michalski 2012). All statistical analyses were performed with R 3.1.3 (R Core Team 2014).

8.1.4 Results

8.1.4.1 The effects of seed weight, life form and dispersal mode on the process of ripening

Median germinule weight of nanophanerophytes was 20 times higher than for herbaceous and 9 times higher than for therophyte species. By contrast, differences in diaspore weight were much higher. Median diaspore weight of nanophanerophytes was 284 times higher than for herbaceous and 102 times higher than for therophyte species. We found that the species' temperature demands for ripening and the diaspore weight were positively and significantly correlated ($p = 0.009$, Table i-1 and Figure i-1) whereby the germinule weight did not show a significant effect on ripening. Species with lightweight diaspores like the herbaceous *Bellis perennis* or *Erigeron annuus* showed the lowest temperature demands for ripening. By contrast, shrub species with high diaspore weight like *Rosa canina* or *Crataegus laevigata* showed the highest temperature demands for ripening (see Figure i-1). Surprisingly, while testing for the correlation between diaspore weight and temperature demands for each life form separately, no significant relationship could be detected.

Table i-1: Summary statistics of the linear models (LM) for the effect of life form and seed weight on cumulative temperature sums for ripening. The model was based on data on cumulative temperature sums for the ripening duration of 104 species. The original model also comprised three interactions between the three weight variables and life form. Due to their insignificance, these interactions were stepwise deleted from the model. The table includes estimates, standard errors (Std. Error), t- and corresponding p-values for all significant interactions and variables. Different symbols indicate significant levels with ***$p < 0.001$ and **$p < 0.01$.

Variable	Estimate	Std. Error	t-value	p-value	
Herbaceous	638.04	44.24	14.423	<0.001	***
Therophytes	-222.03	143.52	-1.547	0.125	
Shrubs	622.39	229.57	2.711	0.008	**
Weight of germinule	3.40	2.36	1.440	0.153	
Weight of the diaspore	2.79	1.04	2.671	0.009	**
Weight of flower head	-0.52	0.40	-1.291	0.200	

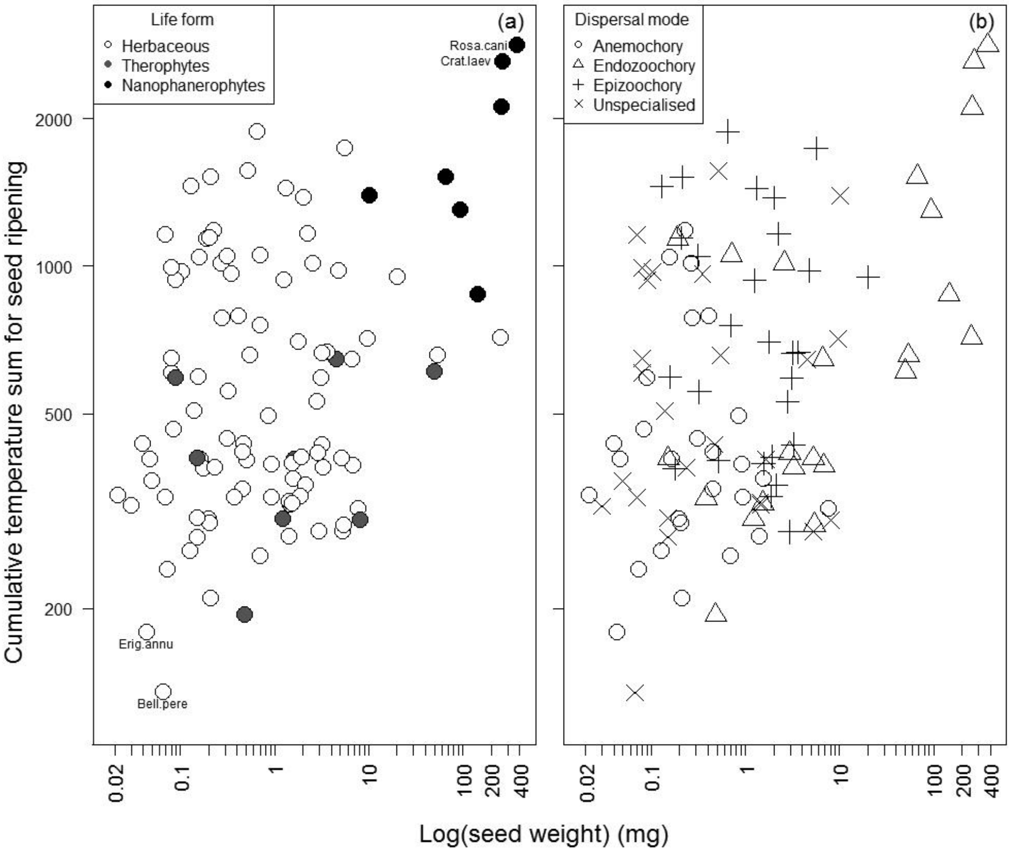

Figure i-1: Relationship between cumulative temperature sum for the ripening duration and seed weight for different life forms (a) and dispersal modes (b). Summary statistics of the LM analysis for the relationship between seed weight and temperature demands for ripening are provided in Table i-A 1. Species abbreviations: Bell.pere = *Bellis perennis*, Crat.laev = *Crataegus laevigata*, Erig.annu = *Erigeron annuus*, Rosa.cani = *Rosa canina*.

For nanophanerophytes, the temperature demands for ripening were about four and three times higher than for therophytes and herbs, respectively (Table i-3, Figure i-2, both differences highly significant with $p < 0.001$). Similarly, nanophanerophytes showed about 100 times higher diaspore weight than therophytes and 300 times higher diaspore weight than herbs (Table i-2, both differences highly significant with $p < 0.001$). We tested for differences in ripening ‘efficiency’ between life forms, and found that the diaspore ripening quotient was generally lowest for nanophanerophytes (most efficient) and highest for herbs (least efficient). For therophytes and herbaceous plants, the diaspore ripening quotient was 25 and 110 times greater (respectively) than for nanophanerophytes (Table i-2). Due to lower between-life form differences in germinule weight than in the diaspore weight, differences in the germinule ripening quotient between life forms were lesser strong pronounced. Furthermore, temperature demands for ripening differed with respect to the dispersal mode of the species. Anemochorous species showed about 40 % lower temperature demands for ripening than epi- and endozoochorous species (Table i-2, both differences significant with $p < 0.01$).

8.1.4.2 Timing of phenological events throughout the year

With flowering in April or May, initiation of flowering was similar for the different life forms, whereby the flowering period of nanophanerophytes was much shorter than for herbaceous and therophyte species and was restricted to early spring (Figure i-3). Diaspore release during wintertime took place in herbaceous and nanophanerophyte species whereas therophyte species showed latest timing of diaspore release in beginning of winter.

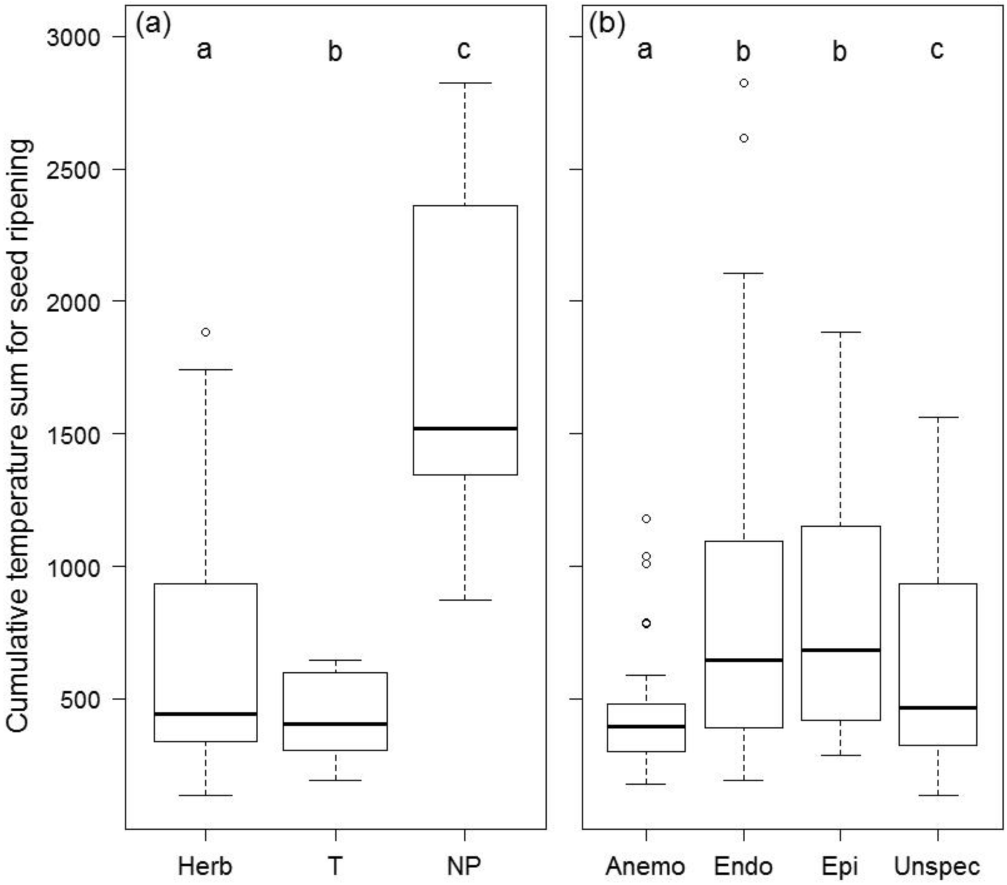

Figure i-2: Cumulative temperature sum for the temperature demands for ripening for 104 species, differentiated by their life form (a) and dispersal mode (b). Letters above the boxes indicate significant differences in temperature demands for ripening between life forms and dispersal mode, respectively, according to summary statistics of LM analyses. Data are shown for 104 species, with 89 herbaceous species ("Herb"), eight therophytes ("T") and seven nanophanerophytes ("NP"). Subfigure (b) shows 27 anemochorous species ("Anemo"), 23 endozoochorous species ("Endo"), 28 epizoochorous species ("Epi") and 26 species without obvious adaptations towards a certain dispersal mode ("Unspec"). According to LM analysis, different letters indicate significant differences (with $p < 0.05$) between factor levels for each plot separately.

Table i-2: Summary table for median values of the variables cumulative temperature sum and duration (days) for diaspore ripening, germinule and diaspore weight, and germinule and diaspore ripening quotient (calculated dividing the cumulative temperature sum for ripening by the weight of the species) differentiated by both the species' life form and dispersal mode. For species-specific values of date, duration (Dur) and cumulative temperature sum (CTS) for flowering, ripening and seed release see Table i-A 7.

	Ripening		**Weight (mg)**		**Ripening quotient**	
	CTS	Dur (days)	Germinule	Diaspore	Germinule	Diaspore
Life form						
Herb	443.95	29.00	0.52	0.52	1075.50	1075.50
T	404.26	25.38	1.18	1.43	325.61	247.93
NP	1521.29	80.76	10.25	146.67	135.67	9.78
Dispersal mode						
Anemochorous	393.64	21.56	0.23	0.23	1894.33	1894.33
Endozoochorous	645.98	48.03	2.94	5.40	249.83	77.06
Epizoochorous	683.30	39.48	1.83	1.83	452.74	452.74
Unspecialised	468.80	31.60	0.19	0.19	2032.26	2032.26

8.1.4.3 Diaspore release phenology

Both, the temperature demands and the duration for diaspore release differed considerably between the species' dispersal mode (Table i-2, Figure i-4). Median diaspore release duration was 60 % higher for anemochorous species, and two times higher for epizoochorous species than for endozoochorous species.

The environmental conditions during diaspore release differed between the dispersal types. Median air temperature during diaspore release of anemochorous species was 3.88 °C higher than for epizoochorous species (Figure i-A 1 on page 118). Median relative humidity during diaspore release of anemochorous species was 8 % lower than for endozoochorous species and 6 % lower than for epizoochorous species. Median precipitation during diaspore release was 2.7 fold higher for endozoochorous species and 53 % higher for epizoochorous species than for anemochorous species.

8.1.4.4 The effect of plant phylogeny on phenology and seed weight

The total set of 104 species analysed in this study originated from 30 different plant families. On average, the number of species per family was 3.5. The plant families with most of the studied species were Asteraceae, Poaceae, Apiaceae and Rosaceae with altogether 52 % of the 104 species (23, 17, 7, and 7 species, respectively). We tested the degree to which phylogeny of the studied species was related to their similarity in phenology and diaspore morphology. Our results show that the species' temperature demands for ripening had a significant phylogenetic effect ($p < 0.001$, Table i-3). For example, for the Rosaceae family, the temperature demands for ripening were 3 times greater than for the Asteraceae family and 2 times greater than for the Poaceae family. Furthermore, diaspore weight, and timing of diaspore release both showed a significant phylogenetic signal ($p = 0.005$, and $p = 0.044$, respectivley).

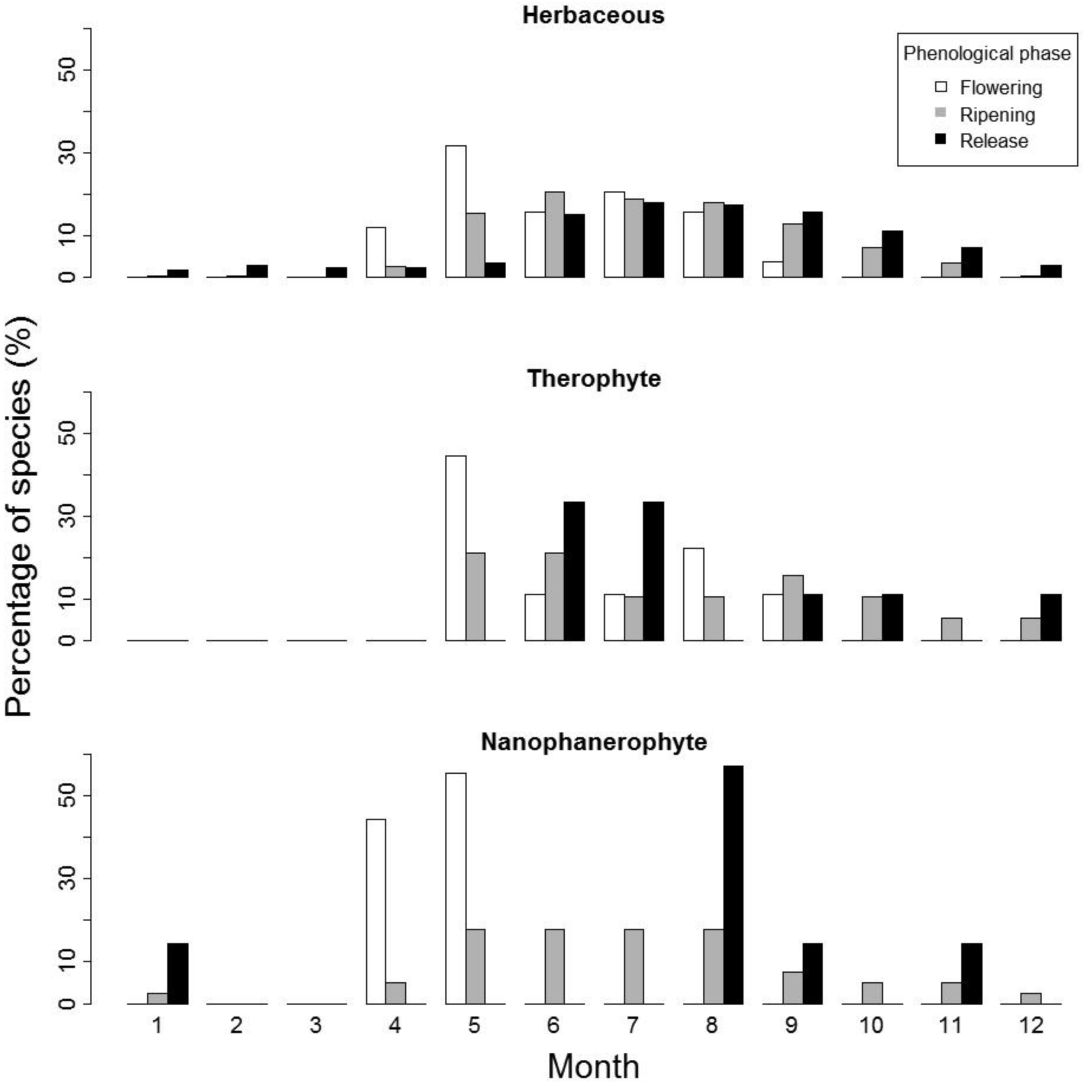

Figure i-3: Percentage of species in the phenological phases flowering (white), ripening (grey), and release (black), differentiated by the life form of the 104 plant species. The number of species was 89, 8 and 7 for herbaceous, therophyte, and nanophanerophyte species, respectively.

8.1.4.5 Phenological response between different years and sites

In order to test for the effect of different growing seasons (years 2009 and 2010) and different locations (three sites on different elevational levels), we performed an analysis based on data from the 'associated monitoring' focusing on 18 species. The environmental variables temperature, relative air humidity and precipitation showed significant differences between all three sites (all differences highly significant with $p < 0.001$, Table i-A 6). With increasing altitude ('Frankfurt' < 'Lower Vogelsberg Mts.' < 'Higher Vogelsberg Mts.'), mean daily temperature decreased while mean relative humidity and mean precipitation increased (Table i-A 6. The temperature demand for seed ripening was significantly lower for the site 'Higher Vogelsberg Mts.' than for the site 'Frankfurt' ($p = 0.038$, Table i-A 6, Figure i-A 2). Between the years 2009 and 2010, we did not find significant differences in temperature demands for seed ripening.

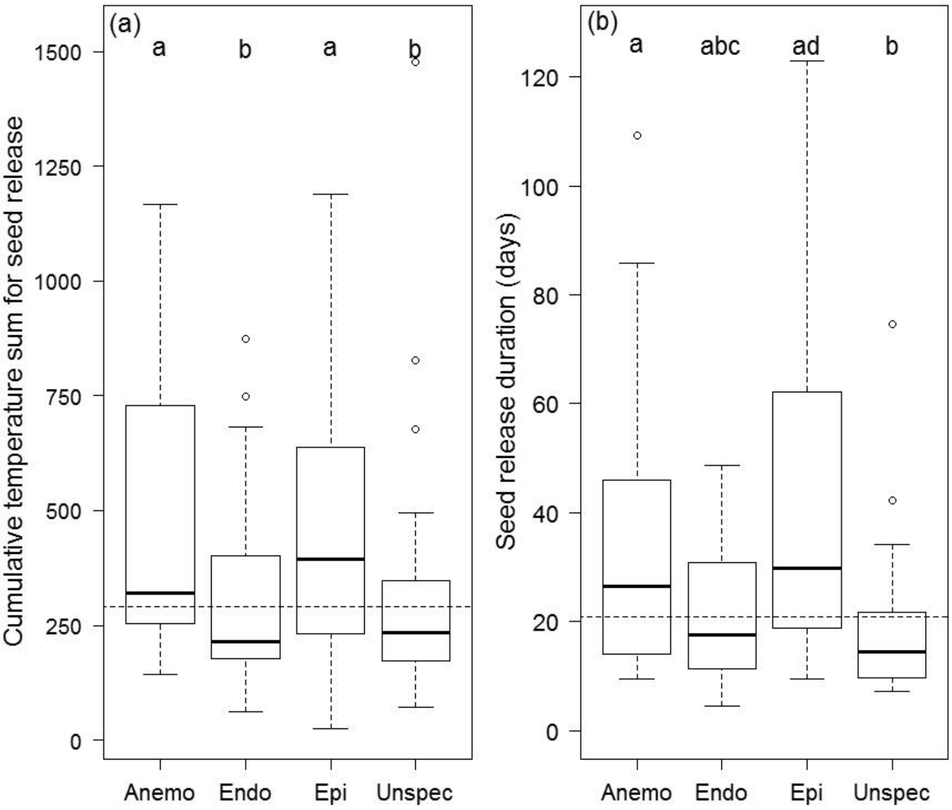

Figure i-4: Temperature demands (a) and duration (b) for diaspore release of 104 Central European species, differentiated by the dispersal mode (see Figure i-2 for number of species per dispersal mode). The dashed line shows the median of the respective variable during the entire period of diaspore release. According to LM analysis, different letters indicate significant differences (with $p < 0.05$) between factor levels for each plot separately.

Table i-3: Summary statistics for a phylogenetic effect on temperature sums of different phenological phases. The analysis was carried out for 104 species. Abbreviations: CTS = cumulative temperature sum, K = k-statistic, PIC: phylogenetically independent contrast, PIC var obs = mean variance of the observed PIC, PIC var rnd = mean variance of the randomized PIC. Different symbols indicate significant levels with ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

Variable	K	PIC var obs	PIC var rnd	z-value	p-value	
Timing of flowering (CTS)	0.195	28866.31	39919.48	-1.108	0.118	
Timing of diaspore release (CTS)	0.200	36003.58	54388.63	-1.441	0.044	*
Duration of flowering (CTS)	0.212	1305.53	2082.13	-1.040	0.087	
Duration of ripening (CTS)	0.378	5408.95	16708.62	-1.750	< 0.001	***
Duration of diaspore release (CTS)	0.125	5656.88	5834.09	-0.096	0.542	
Duration of diaspore release (days)	0.201	24.38	40.43	-1.048	0.094	
Diaspore weight (mg)	0.484	56.43	223.94	-1.151	0.005	**

8.1.5 Discussion

8.1.5.1 Explaining the process of seed ripening: Plant traits and environmental effects

For shrubs, diaspore weight was much higher than for herbaceous and therophyte species. Probably, this is because tall plant species (like shrubs) are able to produce bigger and heavier diaspores (Thompson and Rabinowitz 1989). Likewise, for shrubs the temperature demands for ripening were much higher than for herbaceous and therophyte species. We found a positive and significant correlation between species' diaspore weight and the temperature demands for ripening. Furthermore, we found that this relationship exists only among the life form species groups and not within these groups (Table i-1, Figure i-1). Hence, we suggest that the differences in both diaspore weight and temperature demands for ripening between the life forms are very important for their statistical relationship. Already Primack (1987) argued that species with large diaspores require a greater period for maturation than species with smaller diaspores. The higher temperature demands of woody plants explain the apparent constraint for early flowering of these species as well as the long ripening period between flowering and diaspore release (Figure i-3).

While relating the temperature demands for ripening to the diaspore weight of species, temperature demands for ripening per diaspore weight were lowest for shrub species showed (see Table i-2, ripening quotient). Likewise, differences in the germinule ripening quotient between life forms were apparent but less pronounced than for the diaspore ripening quotient which is clearly due to smaller differences in germinule weight than diaspore weight. The finding of a much more ‘efficient’ ripening process of shrubs than short-lived plant species could possibly be explained by the physiological differences between plant life forms.

When differentiating morphological reproductive structures, differences in the chemical composition between the germinule and the complete diaspore (i.e. including fruit flesh) are apparent. For instance, for species with berry-like diaspores, the germinule often shows higher amounts of lipids and proteins in dry weight than their diaspores with fruit flesh (Bazzaz et al. 1987). Even though the germinule consists of tissue with higher physiological costs (lipids and proteins), the diaspore mass showed a higher correlation with the temperature demands for ripening. In general, reproductive structures of species and life forms are suggested to differ in the chemical composition, quantity of available nutrients, relative mass, and the number of reproductive structures a plant produces (Kochmer and Handel 1986; Bazzaz et al. 1987). With perennial species, which have a higher annual biomass production than short-lived species (Lambers et al. 2008), life forms differ in the proportion of annual metabolic budget that is devoted to reproduction (Bazzaz et al. 1987). Of course, with their woody and perennial life form, shrubs exhibit an extensive and persisting physiological system for growth and reproduction that is likely to explain the more efficient relation of temperature demands for production of diaspore mass.

8.1.5.2 Does the dispersal mode have an effect on the phenology of ripening and diaspore release?

For the studied anemochorous species (mainly Asteraceae species, Table i-A 4), an apparently temperature demanding and (slightly) prolonged diaspore release period was coupled with both higher temperatures and lower relative humidity during diaspore release. Low air humidity clearly has a positive effect on the ability of diaspores to be dispersed by wind. For example, the number of released seeds with pappus is strongly reduced by high humidity in two *Carduus* species (Asteraceae, Jongejans et al. 2007). The combination of low relative humidity and high temperature is likely to promote the generation of convective updrafts (Finnigan and Kaimal 1994) that are highly important for long-distance seed dispersal of herbaceous species with low seed terminal velocity (Tackenberg et al. 2003; Crone et al. 2011). For such species, like for example *Tragopogon dubius*, morphological adaptations are suggested to promote diaspore release during periods showing optimal conditions for dispersal by wind (Greene and Quesada 2011). Likewise, Jongejans et al. (2007) found morphological mechanisms to facilitate a short-term synchronisation of diaspore release with optimal wind conditions and low air humidity. The existence of enhanced conditions for long-distance seed dispersal by wind during diaspore release can be cautiously interpreted as a phenological adaptation i.e. synchronisation with optimal conditions for diaspore release during optimal conditions for wind dispersal. Our result that anemochorous species showed very low temperature demands for ripening is likely related to the low seed weight of the species.

Besides such morphological structures enhancing environmental conditions during diaspore release by short-term synchronisation, phenological adaptations can lead to 'long-term' (e.g. seasonal) synchronisation for diaspore release during optimal periods and thereby positively affect the conditions for seed dispersal. For example, wind-dispersed trees are often suggested to exhibit a seasonal synchronisation of diaspore release with periods offering favourable conditions for dispersal by wind (e.g. Nathan et al. 2000; Heydel et al. 2015). This synchronisation of wind-dispersed plant species can be achieved by means like extended ripening durations for seeds in order to match a particular season that exhibits e.g. higher wind speeds (Hamann 2004; Heydel et al. 2015).

Epizoochorous species showed both, high amounts of temperature demands for seed ripening together with a highly temperature demanding and longer diaspore release duration. Such extended diaspore release duration is suggested to increase dispersal distances of epizoochorous seeds (Lacey 1982) of e.g. *Daucus carota* (Lacey 1980) and may be partially controlled by the parent plant.

Endozoochorous species showed a pattern of high temperature demands for seed ripening together with short dispersal duration. High temperature demands for seed ripening could be explained by much higher weight of seeds (see Table i-2). We found short diaspore release durations of endozoochorous species. For endozoochorous shrub species, these short release durations could possibly be explained by frugivory birds. For the dispersal of endozoochorous seeds, frugivory birds are commonly suggested to cause rapid removal rates of seeds, particularly during fall (Gurevitch et al. 2006; Thompson and Willson 1979; Stiles 1980). Indeed, the seeds of the studied shrub species were released during beginning of fall (mean dispersal date of shrub species 09-21-2009). A further aspect that could have contributed to short diaspore release durations for endozoochorous shrub species could be markedly synchronous seed ripening and release within shrub species with seeds that ripen in fall (Thompson and Willson 1979).

8.1.5.3 How does the species phylogeny affect the phenology?

We found a phylogenetic signal for the duration of ripening and the timing of diaspore release (Table i-3). This finding is in accordance with Crane and Brown (1942) and Larcher (2003) who both stated that the rate of ripening is primarily controlled by internal factors and that environmental cues only seldom stimulate the phenology of fruit ripening. Furthermore, we found that the diaspore weight showed a significant phylogenetic signal. This strongly indicates that the evolutionary history of the species' lineage does shape its diaspore weight and, by implication, the temperature demands for diaspore ripening and timing of release. In accordance, Lord et al. (1995) studied data from six temperate floras and found that the majority of diaspore mass variation within and among the six floras was related to the phylogenetic relatedness of species. Our results also suggest that the timing of flowering is not affected (that much) by the phylogeny of species. Ollerton and Lack (1992) suggested that either selection on flowering time itself is not a strong evolutionary force or that the developmental constraints on flowering phenology are so great that they override any potential natural selection. By contrast, Davies et al. (2013) stated, that according to the flowering times of species, the phenological response of species cannot be treated independently.

8.1.5.4 Reproducibility of our results: Variability of temperature sums for ripening between years and sites

We found no significant differences in temperature demands for ripening between different growing seasons. Hence, we suggest that species-specific results for the temperature demands for the species' reproductive development obtained from this study should be applicable to studies from other years. By contrast, the individuals from the three sites differed in the temperature demands for ripening. The temperature demand for ripening at the sites 'Frankfurt' was significantly higher than the temperature demand at the site 'Higher Vogelsberg Mts.'. Between the three sites, also the mean daily temperature differed significantly: the mean daily temperature was 57 % and 35 % higher at the sites 'Frankfurt' and 'Lower Vogelsberg Mts.', respectively, than at the site 'Higher Vogelsberg Mts.' (differences between sites averaged over both years 2009 and 2010). The lower 'energy demand' of the individuals monitored at the site 'Higher Vogelsberg Mts.' indicates, that the temperature demands within species can differ between different geographical origins. This is likely to be due to physiological adaptations of the individuals at higher sites towards a ripening process that requires less temperature input than at lowland elevations (compare e.g.

Vitasse et al. 2013). The development of seeds with lesser high temperature demands is likely to be an adaptation towards the shorter vegetation period at higher elevations (Rötzer and Chmielewski 2001; Kembel et al. 2010). However, in order to rule out environmental differences in other variables than those studied in our approach, factors like sun shine duration, which is supposed to be not altitude specific, should also be comprised in future studies that assess species phenology along elevational gradients (Körner 2007).

8.1.6 Conclusions

We found evidence for differential effects of plant traits on the ripening and diaspore release phenology. In particular, we found that seed weight is positively correlated with the ripening duration and that differences in the seed weight between different life forms are important for this relationship. Plant species of the shrub life form showed the most efficient ratio of ripening temperature demands and seed weight. With respect to the species evolutionary relatedness, we found phylogenetic signals for the diaspore weight, the temperature demands of ripening, and the timing of diaspore release. This strongly indicates that the evolutionary history of the species' lineage does shape its diaspore weight and, by implication, the temperature demands for diaspore ripening and timing of release. The prevailing environmental conditions during diaspore release of the studied wind-dispersed herb species are likely to enhance dispersal distances of the diaspores. Hence, we tentatively suggest short-term synchronisation of favourable conditions during diaspore release of wind-dispersed herb species as phenological adaptations. Species showed similar temperature demands for ripening in different growing seasons. By contrast, significantly lower temperature demands for ripening of individuals occurring at higher than at lower altitudes indicate physiological adaptations towards less temperature input for seed ripening under conditions of a shortened growing season. In further studies, data on the single flower should be analysed together with phenological data on the population level in order to address research questions related to the onset and timing of phenological phases. For the periods and plant individuals analysed in this paper, respective data on the population level are available and should be comprised in further studies in order to enhance the transferability of the obtained results. As one of few known studies that examine single flower phenology, we were able to capture developmental patterns of late phases for many Central European plant species that are not affected by factors such as population size or environmental heterogeneity. We provided basic knowledge about how ecological factors and phylogeny affect diaspore ripening duration and timing of their release.

Thereby, our study facilitates to take account of climatic effects, e.g. due to climate change, whilst assessing the ripening phenology of plant species.

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8.1.8 Supplementary material

Table i-A 1: Topographical characterisation of study sites and weather stations of the German Meteorological Service. All locations lie within the federal state Hesse in Germany. Abbreviations: AMSL = Height above mean sea level [m].

Site	Type of site	AMSL	Description of location	Latitude	Longitude	DWD Station ID
Frankfurt am Main	Study site	110	Frankfurt am Main	50.13	8.66	N/A
Frankfurt am Main	Weather station	124	Frankfurt/Main-Westend	50.13	8.67	1424
Lower Vogelsberg Mts.	Study site	250	Eichelsdorf (Nidda), Wetteraukreis	50.45	9.07	N/A
Lower Vogelsberg Mts.	Weather station	258	Gründau-Breitenborn	50.27	9.19	1863
Higher Vogelsberg Mts.	Study site	690	Herchenhain, Gemeinde Grebenhain	50.50	9.27	N/A
Higher Vogelsberg Mts.	Weather station	743	Hoherodskopf/Vogelsberg	50.51	9.22	7396

Table i-A 2: Definition of phenological monitoring based on the stage of flower and seed development.

		Developmental stage	
Phenological phase	**Stage**	**Flowers of Dicotyledoneae**	**Flowers of Poaceae**
Flower bud	1	Petals not visible	Inflorescence visible
Flower bud	2	Petals visible	Spikelet visible
Flower bud	3	Opening bud (early)	Glumes individually visible
Flowering	4	Opening bud (later)	Stamina and ovary visible (early)
Flowering	5	Full flowering	Stamina and ovary visible (mid)
Flowering	6	Petals partially detach	Stamina and ovary visible (later)
Ripening	7	Ovary slightly thickened	
Ripening	8	Ovary more strongly thickened	
Ripening	9	Ovary thickened	
Ripening	10	10 % of full ripening achieved	
Ripening	11	30 % of full ripening achieved	
Ripening	12	50 % of full ripening achieved	
Ripening	13	70 % of full ripening achieved	
Ripening	14	100 % of full ripening achieved	
Diaspore release	15	10 % of diaspores released	
Diaspore release	16	30 % of diaspores released	
Diaspore release	17	50 % of diaspores released	
Diaspore release	18	70 % of diaspores released	
Diaspore release	19	100 % of diaspores released	

Table i-A 3: Mean weight of the morphological structures germinule, diaspore and flower head (SD=standard deviation, n=number of measurements).

	Germinule weight (mg)			Diaspore weight (mg)			Flower head weight (mg)				
Species name	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**	**No. of flowers**	**Family**
Achillea millefolium agg.	0.23	0.08	20	0.23	0.08	20	4.39	0.76	10	25	Asteraceae
Achillea ptarmica agg.	0.23	0.08	20	0.23	0.08	20	23.10	4.95	10	39	Asteraceae
Aegopodium podagraria L.	3.11	0.66	10	3.11	0.66	10	NA	NA	NA	25	Apiaceae
Agrimonia eupatoria L.	20.06	5.20	10	20.06	5.20	10	NA	NA	NA	34	Rosaceae
Agrostis capillaris L.	0.05	0.01	10	0.05	0.01	10	NA	NA	NA	25	Poaceae
Allium ursinum L.	6.85	1.24	10	6.85	1.24	10	NA	NA	NA	40	Alliaceae
Ambrosia artemisiifolia L.	4.52	1.41	10	4.52	1.41	10	NA	NA	NA	93	Asteraceae
Anthericum liliago L.	9.66	0.75	10	9.66	0.75	10	128.98	21.56	5	40	Agavaceae
Anthriscus sylvestris agg.	2.98	1.09	10	2.98	1.09	10	NA	NA	NA	25	Apiaceae
Arabis glabra (L.) Bernh.	0.07	0.02	5	0.07	0.02	5	2.15	0.54	5	25	Brassicaceae
Arnica montana L.	1.43	0.20	10	1.43	0.20	10	117.43	13.28	10	25	Asteraceae
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	1.58	0.29	10	1.58	0.29	10	NA	NA	NA	25	Poaceae
Artemisia campestris agg.	0.21	0.04	10	0.21	0.04	10	1.85	0.20	10	17	Asteraceae
Artemisia vulgaris agg.	0.32	0.06	10	0.32	0.06	10	2.51	0.59	10	40	Asteraceae
Atropa bella-donna L.	1.17	0.13	10	253.15	113.78	4	253.15	113.78	4	29	Solanaceae
Bellis perennis L.	0.07	0.02	10	0.07	0.02	10	NA	NA	NA	25	Asteraceae
Betonica officinalis L.	1.46	0.48	10	1.46	0.48	10	5.94	1.96	10	37	Lamiaceae
Brachypodium pinnatum agg.	5.64	0.85	10	5.64	0.85	10	NA	NA	NA	35	Poaceae
Brachypodium sylvaticum (Huds.) P. Beauv.	2.58	0.59	30	2.58	0.59	30	NA	NA	NA	20	Poaceae
Briza media L.	0.46	0.11	10	0.46	0.11	10	NA	NA	NA	25	Poaceae
Campanula baumgartenii Becker	0.07	0.01	10	0.07	0.01	10	11.87	1.71	10	37	Campanulaceae
Campanula rotundifolia agg.	0.05	0.01	30	0.05	0.01	30	9.57	1.69	10	40	Campanulaceae
Cardamine pratensis agg.	1.44	0.59	10	1.44	0.59	10	100.65	42.76	10	38	Brassicaceae
Carduus crispus L.	0.21	0.03	10	0.21	0.03	10	630.71	306.66	10	29	Asteraceae
Carduus nutans agg.	0.16	0.05	10	0.16	0.05	10	5.20	1.64	10	39	Asteraceae
Carex pendula Huds.	1.32	0.11	10	1.32	0.11	10	NA	NA	NA	16	Cyperaceae

	Germinule weight (mg)			Diaspore weight (mg)			Flower head weight (mg)				
Species name	Mean	SD	n	Mean	SD	n	Mean	SD	n	No. of flowers	Family
Carex sylvatica Huds.	1.79	0.18	10	1.79	0.18	10	NA	NA	NA	25	Cyperaceae
Centaurea jacea L. s.l.	2.80	0.79	10	2.80	0.79	10	314.53	32.98	10	37	Asteraceae
Centaurea scabiosa L. s.l.	7.78	1.94	10	7.78	1.94	10	521.72	90.81	10	34	Asteraceae
Circaea lutetiana L.	2.03	0.38	10	2.03	0.38	10	NA	NA	NA	38	Onagraceae
Cirsium palustre (L.) Scop.	0.94	0.43	30	0.94	0.43	30	10.76	1.29	5	37	Asteraceae
Cornus mas L.	154.94	13.20	10	257.86	15.05	10	257.86	15.05	10	40	Cornaceae
Crataegus laevigata (Poir.) DC. s.l.	153.17	52.79	10	267.68	89.96	10	267.68	89.96	10	35	Rosaceae
Crepis biennis L.	0.93	0.28	10	0.93	0.28	10	41.00	9.20	10	40	Asteraceae
Cytisus scoparius (L.) Link	10.25	0.56	10	10.25	0.56	10	333.70	68.28	5	37	Fabaceae
Deschampsia cespitosa agg.	0.28	0.12	20	0.28	0.12	20	NA	NA	NA	30	Poaceae
Deschampsia flexuosa (L.) Trin.	0.16	0.03	8	0.16	0.03	8	NA	NA	NA	25	Poaceae
Dianthus carthusianorum agg.	0.55	0.10	10	0.55	0.10	10	36.29	9.65	10	20	Caryophyllaceae
Digitalis purpurea L.	0.08	0.02	10	0.08	0.02	10	208.42	5.46	5	40	Plantaginaceae
Epilobium angustifolium L.	0.04	0.01	30	0.04	0.01	30	12.60	1.62	10	40	Onagraceae
Erigeron annuus (L.) Pers.	0.04	0.01	10	0.04	0.01	10	12.38	1.43	10	40	Asteraceae
Eryngium campestre L.	2.26	0.68	10	2.26	0.68	10	182.14	45.84	10	36	Apiaceae
Eupatorium cannabinum L.	0.31	0.12	10	0.31	0.12	10	1.85	0.61	10	64	Asteraceae
Festuca rubra agg.	0.18	0.06	10	0.18	0.06	10	NA	NA	NA	25	Poaceae
Filipendula ulmaria (L.) Maxim.	0.52	0.18	30	0.52	0.18	30	NA	NA	NA	42	Rosaceae
Frangula alnus Mill.	24.78	3.52	10	66.97	25.14	10	66.97	25.14	10	40	Rhamnaceae
Geranium robertianum agg.	1.64	0.37	30	1.64	0.37	30	NA	NA	NA	40	Geraniaceae
Geranium sylvaticum L.	5.31	0.59	10	5.31	0.59	10	NA	NA	NA	26	Geraniaceae
Geum rivale L.	1.25	0.20	10	1.25	0.20	10	NA	NA	NA	38	Rosaceae
Glyceria maxima (Hartm.) Holmb.	0.27	0.08	10	0.27	0.08	10	NA	NA	NA	25	Poaceae
Hieracium pilosella L.	0.13	0.01	10	0.13	0.01	10	15.46	2.39	10	40	Asteraceae
Holcus lanatus L.	0.20	0.11	30	0.20	0.11	30	NA	NA	NA	25	Poaceae
Hordelymus europaeus (L.) Jessen ex Harz	6.70	1.33	30	6.70	1.33	30	NA	NA	NA	25	Poaceae

	Germinule weight (mg)			Diaspore weight (mg)			Flower head weight (mg)				
Species name	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**	**No. of flowers**	**Family**
Hordeum secalinum Schreb.	3.27	0.91	10	3.27	0.91	10	NA	NA	NA	40	Poaceae
Hypericum maculatum agg.	0.09	0.05	30	0.09	0.05	30	17.80	0.92	10	38	Hypericaceae
Hypericum perforatum L.	0.08	0.01	10	0.08	0.01	10	11.29	4.06	10	40	Hypericaceae
Impatiens parviflora DC.	8.14	1.71	30	8.14	1.71	30	81.89	20.54	10	41	Balsaminaceae
Knautia arvensis agg.	5.26	1.45	10	5.26	1.45	10	121.81	26.09	10	52	Dipsacaceae
Koeleria pyramidata agg.	0.42	0.15	10	0.42	0.15	10	NA	NA	NA	25	Poaceae
Lamium galeobdolon agg.	2.94	0.52	10	2.94	0.52	10	15.74	3.69	10	22	Lamiaceae
Lapsana communis L.	0.47	0.07	10	0.47	0.07	10	10.24	3.47	10	28	Asteraceae
Leontodon autumnalis L.	0.07	0.03	10	0.07	0.03	10	11.84	1.31	10	48	Asteraceae
Leucanthemum vulgare agg.	0.52	0.09	10	0.52	0.09	10	162.87	54.92	10	35	Asteraceae
Lychnis flos-cuculi L.	0.15	0.03	20	0.15	0.03	20	13.34	3.24	10	40	Caryophyllaceae
Lycopus europaeus L.	0.21	0.04	10	0.21	0.04	10	NA	NA	NA	48	Lamiaceae
Lysimachia vulgaris L.	0.35	0.12	10	0.35	0.12	10	17.95	4.80	6	36	Myrsinaceae
Lythrum salicaria L.	0.16	0.03	10	0.16	0.03	10	11.60	2.96	5	56	Lythraceae
Medicago lupulina L.	0.15	0.03	8	0.15	0.03	8	NA	NA	NA	30	Fabaceae
Molinia caerulea agg.	0.70	0.26	10	0.70	0.26	10	NA	NA	NA	35	Poaceae
Nardus stricta L.	0.65	0.10	10	0.65	0.10	10	NA	NA	NA	25	Poaceae
Papaver dubium agg.	0.09	0.01	10	0.09	0.01	10	88.93	33.73	10	25	Papaveraceae
Pastinaca sativa L.	3.65	0.99	10	3.65	0.99	10	NA	NA	NA	34	Apiaceae
Phragmites australis (Cav.) Trin. ex Steud.	0.08	0.06	10	0.08	0.06	10	NA	NA	NA	25	Poaceae
Phyteuma nigrum F. W. Schmidt	0.15	0.04	30	0.15	0.04	30	4.21	0.84	10	25	Campanulaceae
Phyteuma spicatum L.	0.14	0.05	10	0.14	0.05	10	3.11	1.24	10	25	Campanulaceae
Pimpinella saxifraga agg.	0.32	0.07	10	0.32	0.07	10	NA	NA	NA	45	Apiaceae
Polygonum aviculare agg.	1.22	0.42	10	1.22	0.42	10	NA	NA	NA	20	Polygonaceae
Polygonum bistorta L.	5.40	1.67	30	5.40	1.67	30	NA	NA	NA	25	Polygonaceae
Potentilla erecta (L.) Räusch.	0.38	0.20	30	0.38	0.20	30	NA	NA	NA	40	Rosaceae
Primula elatior agg.	0.71	0.19	10	0.71	0.19	10	65.28	14.21	10	40	Primulaceae

	Germinule weight (mg)			Diaspore weight (mg)			Flower head weight (mg)				
Species name	Mean	SD	n	Mean	SD	n	Mean	SD	n	No. of flowers	Family
Ranunculus acris agg.	1.55	0.60	30	1.55	0.60	30	NA	NA	NA	38	Ranunculaceae
Ranunculus bulbosus agg.	3.22	0.16	10	3.22	0.16	10	NA	NA	NA	39	Ranunculaceae
Ranunculus repens L.	2.14	0.19	10	2.14	0.19	10	NA	NA	NA	25	Ranunculaceae
Rosa canina s.l. L.	8.95	4.73	10	375.07	86.16	10	375.07	86.16	10	32	Rosaceae
Sambucus ebulus L.	18.29	11.49	4	54.25	33.97	4	54.25	33.97	4	44	Adoxaceae
Sambucus nigra L.	2.80	0.92	10	146.67	11.47	10	146.67	11.47	10	38	Adoxaceae
Sanicula europaea L.	4.76	1.61	10	4.76	1.61	10	NA	NA	NA	40	Apiaceae
Saxifraga granulata L.	0.03	0.01	10	0.03	0.01	10	7.74	0.90	10	24	Saxifragaceae
Scabiosa columbaria agg.	1.87	0.75	10	1.87	0.75	10	100.53	34.39	10	23	Dipsacaceae
Scrophularia nodosa L.	0.08	0.02	30	0.08	0.02	30	60.70	10.92	5	40	Scrophulariaceae
Senecio ovatus (P. Gaertn.. B. Mey. & Scherb.) Willd.	0.86	0.29	30	0.86	0.29	30	13.32	1.56	10	40	Asteraceae
Silaum silaus (L.) Schinz & Thell.	3.21	0.79	10	3.21	0.79	10	NA	NA	NA	40	Apiaceae
Solanum nigrum L.	1.15	0.14	10	50.40	14.23	3	50.40	14.23	3	23	Solanaceae
Solidago canadensis L.	0.02	0.01	10	0.02	0.01	10	1.74	0.64	10	40	Asteraceae
Solidago virgaurea L.	0.46	0.05	10	0.46	0.05	10	13.80	2.13	10	40	Asteraceae
Sonchus palustris L.	0.71	0.05	10	0.71	0.05	10	167.78	32.39	10	39	Asteraceae
Sorbus aucuparia L.	3.07	0.23	10	94.81	18.24	10	94.81	18.24	10	37	Rosaceae
Stachys palustris L.	1.53	0.19	20	1.53	0.19	20	6.43	0.80	10	40	Lamiaceae
Succisa pratensis Moench	1.93	0.21	10	1.93	0.21	10	NA	NA	NA	40	Dipsacaceae
Trifolium campestre Schreb.	0.48	0.17	10	0.48	0.17	10	NA	NA	NA	23	Fabaceae
Trisetum flavescens agg.	0.21	0.05	10	0.21	0.05	10	NA	NA	NA	25	Poaceae
Verbascum lychnitis L.	0.10	0.04	10	0.10	0.04	10	NA	NA	NA	32	Scrophulariaceae
Veronica chamaedrys s.str. L.	0.19	0.04	10	0.19	0.04	10	NA	NA	NA	28	Plantaginaceae
Veronica officinalis L.	0.13	0.02	10	0.13	0.02	10	NA	NA	NA	23	Plantaginaceae

Table i-A 4: Seed terminal velocity (Vterm) and diaspore morphology of species obtained from Hintze et al. (2013). Abbreviations: NC = nutrient containing, Mu = Mucilaginous.

			Diaspore appendages						
Species name	**V_{term} (m/s)**	**NC**	**Flat**	**Elongated**	**Hook**	**Mu**	**Missing**	**Dispersal mode**	**Family**
Achillea millefolium agg.	1.25	1	1	1	1	0	0	Unspecialised	Asteraceae
Achillea ptarmica agg.	0.69	0	1	0	0	0	0	Anemochory	Asteraceae
Aegopodium podagraria L.	4.32	0	0	0	0	0	1	Epizoochory	Apiaceae
Agrimonia eupatoria L.	2.96	0	1	0	0	0	0	Epizoochory	Rosaceae
Agrostis capillaris L.	0.89	1	0	0	0	0	0	Anemochory	Poaceae
Allium ursinum L.	9.36	0	0	0	0	0	1	Endozoochory	Alliaceae
Ambrosia artemisiifolia L.	7.29	0	0	0	0	0	1	Unspecialised	Asteraceae
Anthericum liliago L.	3.13	0	0	0	0	0	1	Unspecialised	Agavaceae
Anthriscus sylvestris agg.	5.08	0	0	1	0	0	0	Epizoochory	Apiaceae
Arabis glabra (L.) Bernh.	1.80	0	0	0	0	0	1	Unspecialised	Brassicaceae
Arnica montana L.	0.83	1	1	0	0	1	0	Anemochory	Asteraceae
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	1.55	0	0	1	0	0	0	Anemochory	Poaceae
Artemisia campestris agg.	2.35	0	0	0	0	0	1	Epizoochory	Asteraceae
Artemisia vulgaris agg.	2.02	0	0	1	0	0	0	Epizoochory	Asteraceae
Atropa bella-donna L.	NA	0	0	1	0	0	0	Endozoochory	Solanaceae
Bellis perennis L.	1.38	0	1	0	0	0	0	Unspecialised	Asteraceae
Betonica officinalis L.	2.06	0	0	0	0	0	1	Unspecialised	Lamiaceae
Brachypodium pinnatum agg.	2.14	0	0	0	0	0	1	Epizoochory	Poaceae
Brachypodium sylvaticum (Huds.) P. Beauv.	3.33	0	0	1	0	0	0	Endozoochory	Poaceae
Briza media L.	1.69	0	0	1	1	0	0	Anemochory	Poaceae
Campanula baumgartenii Becker	1.73	1	0	0	0	0	0	Unspecialised	Campanulaceae
Campanula rotundifolia agg.	1.64	1	0	0	0	0	0	Unspecialised	Campanulaceae
Cardamine pratensis agg.	2.52	0	0	1	0	0	0	Unspecialised	Brassicaceae

Species name	V_{term} (m/s)	Diaspore appendages						Dispersal mode	Family
		NC	Flat	Elongated	Hook	Mu	Missing		
Carduus crispus L.	0.40	1	1	0	0	0	0	Anemochory	Asteraceae
Carduus nutans agg.	2.58	0	0	0	0	0	1	Epizoochory	Asteraceae
Carex pendula Huds.	3.43	0	0	0	0	1	0	Epizoochory	Cyperaceae
Carex sylvatica Huds.	3.03	0	0	1	1	0	0	Epizoochory	Cyperaceae
Centaurea jacea L. s.l.	3.90	0	0	0	0	0	1	Epizoochory	Asteraceae
Centaurea scabiosa L. s.l.	1.68	1	0	1	0	0	0	Anemochory	Asteraceae
Circaea lutetiana L.	NA	0	1	1	0	0	0	Epizoochory	Onagraceae
Cirsium palustre (L.) Scop.	0.36	0	0	1	0	0	0	Anemochory	Asteraceae
Cornus mas L.	16.18	0	0	1	0	0	0	Endozoochory	Cornaceae
Crataegus laevigata (Poir.) DC. s.l.	NA	0	0	1	0	0	0	Endozoochory	Rosaceae
Crepis biennis L.	0.68	1	1	0	0	0	0	Anemochory	Asteraceae
Cytisus scoparius (L.) Link	10.00	0	1	0	0	0	0	Unspecialised	Fabaceae
Deschampsia cespitosa agg.	1.28	0	0	0	0	0	0	Anemochory	Poaceae
Deschampsia flexuosa (L.) Trin.	1.31	0	0	1	1	0	0	Anemochory	Poaceae
Dianthus carthusianorum agg.	2.38	0	0	0	0	1	0	Unspecialised	Caryophyllaceae
Digitalis purpurea L.	1.75	0	0	0	0	0	1	Unspecialised	Plantaginaceae
Epilobium angustifolium L.	0.08	1	1	1	0	0	0	Anemochory	Onagraceae
Erigeron annuus (L.) Pers.	NA	0	0	1	0	0	0	Anemochory	Asteraceae
Eryngium campestre L.	2.15	1	0	0	0	0	0	Epizoochory	Apiaceae
Eupatorium cannabinum L.	0.36	0	0	0	0	0	1	Anemochory	Asteraceae
Festuca rubra agg.	2.20	1	1	1	0	0	0	Epizoochory	Poaceae
Filipendula ulmaria (L.) Maxim.	1.73	1	1	1	0	0	0	Unspecialised	Rosaceae
Frangula alnus Mill.	10.89	0	0	1	0	0	0	Endozoochory	Rhamnaceae
Geranium robertianum agg.	NA	0	0	0	0	0	1	Unspecialised	Geraniaceae
Geranium sylvaticum L.	2.93	0	0	1	0	0	0	Unspecialised	Geraniaceae

		Diaspore appendages							
Species name	V_{term} (m/s)	NC	Flat	Elongated	Hook	Mu	Missing	Dispersal mode	Family
Geum rivale L.	1.79	1	1	1	0	0	0	Epizoochory	Rosaceae
Glyceria maxima (Hartm.) Holmb.	0.88	1	0	0	0	0	0	Anemochory	Poaceae
Hieracium pilosella L.	0.45	1	1	1	1	0	0	Anemochory	Asteraceae
Holcus lanatus L.	1.18	1	0	0	0	0	0	Anemochory	Poaceae
Hordelymus europaeus (L.) Jessen ex Harz	2.24	0	0	0	0	0	1	Endozoochory	Poaceae
Hordeum secalinum Schreb.	6.97	0	0	1	0	0	0	Endozoochory	Poaceae
Hypericum maculatum agg.	1.59	1	0	0	0	0	0	Unspecialised	Hypericaceae
Hypericum perforatum L.	1.34	1	0	0	0	0	0	Unspecialised	Hypericaceae
Impatiens parviflora DC.	7.59	0	0	1	0	0	0	Unspecialised	Balsaminaceae
Knautia arvensis agg.	2.90	0	1	0	0	0	0	Endozoochory	Dipsacaceae
Koeleria pyramidata agg.	0.76	0	0	1	0	0	0	Anemochory	Poaceae
Lamium galeobdolon agg.	4.43	0	0	0	0	0	1	Endozoochory	Lamiaceae
Lapsana communis L.	3.87	0	0	1	1	0	0	Unspecialised	Asteraceae
Leontodon autumnalis L.	0.87	1	1	1	0	0	0	Anemochory	Asteraceae
Leucanthemum vulgare agg.	2.58	0	0	0	0	1	0	Epizoochory	Asteraceae
Lychnis flos-cuculi L.	2.52	0	0	0	0	0	1	Unspecialised	Caryophyllaceae
Lycopus europaeus L.	2.19	1	0	0	0	0	0	Epizoochory	Lamiaceae
Lysimachia vulgaris L.	2.70	0	0	1	1	0	0	Unspecialised	Myrsinaceae
Lythrum salicaria L.	1.61	0	0	0	0	1	0	Anemochory	Lythraceae
Medicago lupulina L.	3.80	0	0	1	0	0	0	Endozoochory	Fabaceae
Molinia caerulea agg.	2.06	1	0	0	0	0	0	Epizoochory	Poaceae
Nardus stricta L.	NA	0	0	0	0	0	1	Epizoochory	Poaceae
Papaver dubium agg.	NA	0	0	0	0	0	1	Anemochory	Papaveraceae
Pastinaca sativa L.	2.06	1	1	1	1	0	0	Epizoochory	Apiaceae
Phragmites australis (Cav.) Trin. ex Steud.	0.17	0	0	1	0	0	0	Anemochory	Poaceae

Species name	**V_{term} (m/s)**	**Diaspore appendages** **NC**	**Flat**	**Elongated**	**Hook**	**Mu**	**Missing**	**Dispersal mode**	**Family**
Phyteuma nigrum F. W. Schmidt	NA	0	0	0	0	0	1	Unspecialised	Campanulaceae
Phyteuma spicatum L.	NA	0	0	0	0	0	1	Unspecialised	Campanulaceae
Pimpinella saxifraga agg.	2.47	0	0	0	0	0	1	Epizoochory	Apiaceae
Polygonum aviculare agg.	NA	0	0	0	0	0	1	Endozoochory	Polygonaceae
Polygonum bistorta L.	3.86	0	0	0	0	0	1	Endozoochory	Polygonaceae
Potentilla erecta (L.) Räusch.	1.99	1	1	1	1	0	0	Endozoochory	Rosaceae
Primula elatior agg.	4.62	0	0	1	0	0	0	Endozoochory	Primulaceae
Ranunculus acris agg.	2.34	1	0	0	0	0	0	Epizoochory	Ranunculaceae
Ranunculus bulbosus agg.	2.33	0	1	0	0	0	0	Epizoochory	Ranunculaceae
Ranunculus repens L.	2.58	0	0	1	0	0	0	Epizoochory	Ranunculaceae
Rosa canina s.l. L.	12.32	1	1	0	0	0	0	Endozoochory	Rosaceae
Sambucus ebulus L.	NA	1	0	0	0	0	0	Endozoochory	Adoxaceae
Sambucus nigra L.	NA	1	1	0	0	0	0	Endozoochory	Adoxaceae
Sanicula europaea L.	5.89	0	0	0	0	0	1	Epizoochory	Apiaceae
Saxifraga granulata L.	0.90	0	0	1	0	0	0	Unspecialised	Saxifragaceae
Scabiosa columbaria agg.	2.18	1	0	0	0	0	0	Epizoochory	Dipsacaceae
Scrophularia nodosa L.	NA	0	0	0	0	0	1	Unspecialised	Scrophulariaceae
Senecio ovatus (P. Gaertn.. B. Mey. & Scherb.) Willd.	0.55	1	1	0	0	0	0	Anemochory	Asteraceae
Silaum silaus (L.) Schinz & Thell.	3.42	0	0	1	0	0	0	Epizoochory	Apiaceae
Solanum nigrum L.	NA	1	1	1	0	0	0	Endozoochory	Solanaceae
Solidago canadensis L.	0.32	0	0	1	0	0	0	Anemochory	Asteraceae
Solidago virgaurea L.	0.52	0	0	1	0	0	0	Anemochory	Asteraceae
Sonchus palustris L.	NA	0	0	0	0	0	1	Anemochory	Asteraceae
Sorbus aucuparia L.	NA	1	1	1	0	0	0	Endozoochory	Rosaceae
Stachys palustris L.	3.54	0	0	1	0	0	0	Endozoochory	Lamiaceae

		Diaspore appendages							
Species name	**V_{term} (m/s)**	**NC**	**Flat**	**Elongated**	**Hook**	**Mu**	**Missing**	**Dispersal mode**	**Family**
Succisa pratensis Moench	2.32	1	0	0	0	0	0	Epizoochory	Dipsacaceae
Trifolium campestre Schreb.	1.52	1	1	1	0	0	0	Endozoochory	Fabaceae
Trisetum flavescens agg.	0.78	1	1	1	0	0	0	Anemochory	Poaceae
Verbascum lychnitis L.	2.09	0	0	0	0	0	1	Unspecialised	Scrophulariaceae
Veronica chamaedrys s.str. L.	2.68	1	1	0	0	0	0	Endozoochory	Plantaginaceae
Veronica officinalis L.	NA	0	0	0	0	1	0	Epizoochory	Plantaginaceae

Table i-A 5: Species number for each dispersal mode, differentiated by the life form of the species. Values in parenthesis provide the proportion of species number within each life form.

Dispersal mode	**Herbaceous**		**Therophytes**		**Shrubs**	
Anemochorous	26	(29.2)	1	(12.5)	0	(0)
Endozoochorous	13	(14.6)	4	(50)	6	(85.7)
Epizoochorous	28	(31.5)	0	(0)	0	(0)
Unspecialised	22	(24.7)	3	(37.5)	1	(14.3)

Table i-A 6: Environmental data for temperature and relative humidity (both measured as daily averages), and precipitation as daily sum for three sites and two years (2009 and 2010).

Measure	Site	Temperature	Humidity	Precipitation
Min	Frankfurt	-12.20	37.79	0.00
Min	Lower Vogelsberg Mts.	-15.00	36.00	0.00
Min	Higher Vogelsberg Mts.	-18.40	31.00	0.00
Median	Frankfurt	11.30	73.00	0.00
Median	Lower Vogelsberg Mts.	9.60	81.00	0.10
Median	Higher Vogelsberg Mts.	6.90	89.67	0.30
Mean	Frankfurt	10.73	71.55	1.87
Mean	Lower Vogelsberg Mts.	9.06	78.08	2.44
Mean	Higher Vogelsberg Mts.	6.11	85.05	2.75
Max	Frankfurt	28.50	94.00	40.10
Max	Lower Vogelsberg Mts.	26.90	99.00	49.20
Max	Higher Vogelsberg Mts.	26.00	100.00	48.70

Table i-A 7: Calculated mean values for date, duration and cumulative temperature sum (CTS) for species' phenological phases flowering, ripening and seed release. Abbreviations of phenological phases with Fl = flowering, Ri = ripening, Sr = seed release and life forms (LF) with H = herbaceous, NP = nanophanerophyte, T = therophyte.

	Date		**Duration (days)**			**CTS**				
Species name	**Fl**	**Sr**	**Fl**	**Ri**	**Sr**	**Fl**	**Ri**	**Sr**	**LF**	**Family**
Achillea millefolium agg.	19.6	25.8	37.18	20.32	42.26	687.06	387.42	826.16	H	Asteraceae
Achillea ptarmica agg.	25.7	3.12	41.92	91.58	26.50	859.38	1178.40	163.28	H	Asteraceae
Aegopodium podagraria L.	1.6	28.7	24.50	30.18	12.80	386.70	591.52	260.92	H	Apiaceae
Agrimonia eupatoria L.	29.7	3.11	9.01	73.60	15.10	175.54	950.71	103.24	H	Rosaceae
Agrostis capillaris L.	22.6	23.8	20.50	21.56	44.18	408.70	403.25	871.25	H	Poaceae
Allium ursinum L.	26.4	10.6	9.00	23.61	12.66	113.20	391.44	195.66	H	Alliaceae
Ambrosia artemisiifolia L.	22.8	20.10	9.05	44.47	7.16	174.08	644.35	72.31	T	Asteraceae
Anthericum liliago L.	19.5	16.7	11.50	39.98	7.73	200.20	710.36	146.76	H	Agavaceae
Anthriscus sylvestris agg.	10.5	8.7	34.00	18.71	29.25	541.41	286.70	595.01	H	Apiaceae
Arabis glabra (L.) Bernh.	7.5	27.7	4.90	64.86	18.24	65.60	1157.19	355.63	H	Brassicaceae
Arnica montana L.	24.5	1.7	11.00	17.58	14.02	177.60	280.48	277.47	H	Asteraceae
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	11.5	26.6	25.96	22.43	30.35	411.78	368.21	553.96	H	Poaceae
Artemisia campestris agg.	19.8	23.2	11.71	141.79	34.50	223.75	1142.89	23.70	H	Asteraceae
Artemisia vulgaris agg.	20.7	4.11	45.00	70.55	30.60	913.50	1048.22	254.52	H	Asteraceae
Atropa bella-donna L.	22.8	7.11	16.07	56.36	10.34	294.60	714.91	99.24	H	Solanaceae
Bellis perennis L.	27.4	17.5	14.00	10.00	10.00	182.80	134.70	147.60	H	Asteraceae
Betonica officinalis L.	11.8	15.9	9.89	16.71	19.76	206.58	325.75	290.63	H	Lamiaceae
Brachypodium pinnatum agg.	15.6	20.11	30.79	111.69	39.01	586.77	1741.91	234.29	H	Poaceae
Brachypodium sylvaticum (Huds.) P. Beauv.	8.7	5.10	9.00	60.40	33.70	173.70	1013.31	202.58	H	Poaceae
Briza media L.	31.5	15.7	19.50	19.00	13.50	297.10	350.40	256.10	H	Poaceae
Campanula baumgartenii Becker	19.7	22.8	14.27	15.89	9.84	281.35	337.25	211.18	H	Campanulaceae
Campanula rotundifolia agg.	25.5	7.7	10.71	22.06	14.25	161.09	363.71	293.57	H	Campanulaceae
Cardamine pratensis agg.	22.7	1.9	22.71	17.03	26.32	449.52	329.79	490.66	H	Brassicaceae
Carduus crispus L.	15.7	16.8	14.93	15.77	20.61	294.33	298.15	441.37	H	Asteraceae
Carduus nutans agg.	9.4	7.6	11.95	39.55	10.50	187.48	593.92	151.70	H	Asteraceae

	Date		Duration (days)			CTS				
Species name	**Fl**	**Sr**	**Fl**	**Ri**	**Sr**	**Fl**	**Ri**	**Sr**	**LF**	**Family**
Carex pendula Huds.	18.5	22.8	9.31	75.97	10.84	158.76	1443.21	227.03	H	Cyperaceae
Carex sylvatica Huds.	4.5	12.7	12.00	39.40	38.56	169.70	700.26	678.20	H	Cyperaceae
Centaurea jacea L. s.l.	8.8	1.10	5.86	28.12	31.85	108.16	529.28	410.39	H	Asteraceae
Centaurea scabiosa L. s.l.	11.5	23.6	30.19	19.07	14.47	478.77	319.23	251.63	H	Asteraceae
Circaea lutetiana L.	6.7	10.10	6.39	83.78	9.62	111.34	1380.62	114.18	H	Onagraceae
Cirsium palustre (L.) Scop.	9.7	16.8	19.69	16.66	18.62	386.01	336.71	385.22	H	Asteraceae
Cornus mas L.	1.4	3.9	11.00	122.09	22.19	178.70	2107.06	433.25	NP	Cornaceae
Crataegus laevigata (Poir.) DC. s.l.	24.4	23.11	18.00	170.53	31.06	243.20	2617.96	289.51	NP	Rosaceae
Crepis biennis L.	13.5	15.7	17.85	23.66	52.49	286.70	393.64	1022.61	H	Asteraceae
Cytisus scoparius (L.) Link	10.5	6.8	6.18	75.69	10.68	80.74	1390.66	196.65	NP	Fabaceae
Deschampsia cespitosa agg.	20.6	10.9	16.25	38.42	53.63	318.30	784.07	920.05	H	Poaceae
Deschampsia flexuosa (L.) Trin.	15.6	7.8	7.00	19.10	47.70	115.90	403.71	949.04	H	Poaceae
Dianthus carthusianorum agg.	24.5	20.7	11.00	35.80	15.85	177.60	657.73	314.39	H	Caryophyllaceae
Digitalis purpurea L.	26.5	28.7	10.00	32.00	34.20	152.70	605.10	677.91	H	Plantaginaceae
Epilobium angustifolium L.	2.7	10.8	8.50	22.28	14.03	166.70	433.31	293.04	H	Onagraceae
Erigeron annuus (L.) Pers.	14.6	6.7	15.00	10.75	10.75	248.80	178.50	227.20	H	Asteraceae
Eryngium campestre L.	18.7	8.12	30.93	76.56	97.54	621.79	1163.91	379.63	H	Apiaceae
Eupatorium cannabinum L.	11.8	10.10	25.31	29.91	32.42	498.81	443.95	419.97	H	Asteraceae
Festuca rubra agg.	15.5	22.7	26.16	23.44	55.52	427.56	385.56	1100.91	H	Poaceae
Filipendula ulmaria (L.) Maxim.	30.6	12.10	7.50	88.38	9.43	150.20	1563.01	121.55	H	Rosaceae
Frangula alnus Mill.	2.5	14.8	17.00	80.76	10.11	244.40	1521.29	208.94	NP	Rhamnaceae
Geranium robertianum agg.	21.5	26.6	2.50	25.70	8.28	39.90	403.73	141.36	T	Geraniaceae
Geranium sylvaticum L.	24.5	29.6	11.81	18.00	8.27	189.44	287.01	172.78	H	Geraniaceae
Geum rivale L.	6.5	4.8	6.00	53.32	51.11	88.20	933.84	852.84	H	Rosaceae
Glyceria maxima (Hartm.) Holmb.	5.7	15.10	5.50	49.68	85.90	83.60	1011.34	1030.72	H	Poaceae
Hieracium pilosella L.	11.5	14.6	9.84	15.66	9.50	148.88	261.89	151.88	H	Asteraceae
Holcus lanatus L.	15.5	19.6	18.00	17.55	19.65	300.20	303.86	320.41	H	Poaceae
Hordelymus europaeus (L.) Jessen ex Harz	9.6	10.8	8.50	32.90	32.48	136.70	645.98	682.68	H	Poaceae

	Date		Duration (days)			CTS				
Species name	**Fl**	**Sr**	**Fl**	**Ri**	**Sr**	**Fl**	**Ri**	**Sr**	**LF**	**Family**
Hordeum secalinum Schreb.	12.6	24.7	17.65	19.85	10.90	315.27	387.59	207.08	H	Poaceae
Hypericum maculatum agg.	2.7	6.9	6.50	46.30	19.25	117.30	934.78	340.91	H	Hypericaceae
Hypericum perforatum L.	15.7	23.9	9.00	49.85	15.15	175.00	992.32	252.39	H	Hypericaceae
Impatiens parviflora DC.	20.8	25.9	7.15	17.72	11.96	138.84	303.10	201.70	T	Balsaminaceae
Knautia arvensis agg.	16.8	29.9	14.28	22.55	17.52	278.98	405.31	253.20	H	Dipsacaceae
Koeleria pyramidata agg.	7.6	25.8	5.00	40.16	59.84	80.40	789.18	1167.22	H	Poaceae
Lamium galeobdolon agg.	14.4	26.5	8.50	29.00	4.50	112.79	414.38	80.80	H	Lamiaceae
Lapsana communis L.	14.9	18.11	13.21	38.65	23.58	195.73	432.48	99.14	H	Asteraceae
Leontodon autumnalis L.	9.9	15.10	12.96	16.86	14.33	203.75	240.67	144.20	H	Asteraceae
Leucanthemum vulgare agg.	14.5	6.7	23.30	23.31	28.96	379.75	400.46	563.49	H	Asteraceae
Lychnis flos-cuculi L.	7.5	17.6	11.50	18.50	14.40	164.00	306.30	242.18	H	Caryophyllaceae
Lycopus europaeus L.	11.7	21.12	13.21	90.19	120.92	258.24	1519.08	459.39	H	Lamiaceae
Lysimachia vulgaris L.	6.7	24.9	19.61	51.71	14.82	375.56	964.49	223.98	H	Myrsinaceae
Lythrum salicaria L.	22.6	26.10	24.55	51.38	109.32	466.62	1039.20	989.66	H	Lythraceae
Medicago lupulina L.	24.5	17.7	8.91	25.06	37.14	137.79	404.78	747.29	T	Fabaceae
Molinia caerulea agg.	25.7	23.11	16.71	41.29	122.89	337.43	755.97	806.87	H	Poaceae
Nardus stricta L.	15.5	12.10	31.00	98.86	83.34	503.30	1882.43	729.76	H	Poaceae
Papaver dubium agg.	5.5	30.6	5.78	36.72	26.70	78.23	589.58	524.62	T	Papaveraceae
Pastinaca sativa L.	5.8	2.10	7.00	35.00	22.09	150.40	666.33	323.85	H	Apiaceae
Phragmites australis (Cav.) Trin. ex Steud.	29.8	13.12	46.00	46.12	59.48	863.30	462.84	319.58	H	Poaceae
Phyteuma nigrum F. W. Schmidt	6.5	14.6	7.70	16.80	21.70	111.64	279.68	348.38	H	Campanulaceae
Phyteuma spicatum L.	29.4	22.6	5.00	31.20	27.40	67.20	505.12	493.90	H	Campanulaceae
Pimpinella saxifraga agg.	22.8	24.10	18.77	35.81	23.49	363.27	553.68	210.05	H	Apiaceae
Polygonum aviculare agg.	20.6	20.7	25.90	14.75	14.75	497.05	304.64	285.68	T	Polygonaceae
Polygonum bistorta L.	9.5	15.6	13.88	17.52	11.40	211.82	296.08	181.87	H	Polygonaceae
Potentilla erecta (L.) Räusch.	9.5	22.6	12.11	20.83	21.15	185.18	336.22	370.48	H	Rosaceae
Primula elatior agg.	2.4	4.7	5.50	68.46	33.54	75.30	1053.88	641.76	H	Primulaceae
Ranunculus acris agg.	6.5	25.6	10.71	23.94	23.99	157.89	395.18	439.93	H	Ranunculaceae

	Date		Duration (days)			CTS				
Species name	**Fl**	**Sr**	**Fl**	**Ri**	**Sr**	**Fl**	**Ri**	**Sr**	**LF**	**Family**
Ranunculus bulbosus agg.	1.5	17.6	12.21	26.78	12.55	171.19	432.41	208.78	H	Ranunculaceae
Ranunculus repens L.	10.5	25.7	14.00	22.80	74.88	239.00	357.42	1190.04	H	Ranunculaceae
Rosa canina s.l. L.	21.5	28.1	10.22	213.58	30.64	175.33	2822.81	60.83	NP	Rosaceae
Sambucus ebulus L.	23.8	10.11	10.95	59.02	13.53	209.54	657.92	88.83	H	Adoxaceae
Sambucus nigra L.	15.5	6.8	24.83	48.03	23.41	408.78	875.03	466.85	NP	Adoxaceae
Sanicula europaea L.	6.5	28.7	20.50	54.23	26.00	296.70	979.38	513.95	H	Apiaceae
Saxifraga granulata L.	9.5	17.6	7.50	19.50	12.00	100.30	323.50	199.40	H	Saxifragaceae
Scabiosa columbaria agg.	11.8	24.9	19.43	18.82	19.71	411.55	339.09	251.00	H	Dipsacaceae
Scrophularia nodosa L.	11.5	6.8	8.95	38.13	74.55	144.44	647.41	1476.17	H	Scrophulariaceae
Senecio ovatus (P. Gaertn.. B. Mey. & Scherb.) Willd.	20.7	9.9	20.90	24.17	17.89	421.21	494.72	284.45	H	Asteraceae
Silaum silaus (L.) Schinz & Thell.	3.7	26.9	16.88	32.73	68.85	331.02	664.85	892.08	H	Apiaceae
Solanum nigrum L.	13.9	31.12	10.98	77.43	23.26	162.27	609.13	73.07	T	Solanaceae
Solidago canadensis L.	23.7	7.9	37.80	16.46	10.66	771.05	340.09	186.64	H	Asteraceae
Solidago virgaurea L.	23.8	19.10	13.93	26.55	36.10	266.65	416.85	308.35	H	Asteraceae
Sonchus palustris L.	7.8	1.9	7.49	12.24	9.65	163.54	256.21	182.33	H	Asteraceae
Sorbus aucuparia L.	2.5	9.8	23.08	69.66	9.42	353.20	1298.18	175.39	NP	Rosaceae
Stachys palustris L.	8.7	30.8	9.00	16.38	48.68	173.70	328.08	873.10	H	Lamiaceae
Succisa pratensis Moench	31.8	21.11	15.35	28.89	83.26	262.26	407.77	499.04	H	Dipsacaceae
Trifolium campestre Schreb.	26.5	19.6	6.97	12.42	11.53	115.09	194.19	213.36	T	Fabaceae
Trisetum flavescens agg.	31.5	12.7	18.00	12.50	28.98	277.10	209.80	586.29	H	Poaceae
Verbascum lychnitis L.	7.6	12.8	9.80	48.99	9.12	156.00	972.08	186.69	H	Scrophulariaceae
Veronica chamaedrys s.str. L.	20.4	15.7	12.80	66.73	11.63	183.13	1137.58	218.01	H	Plantaginaceae
Veronica officinalis L.	26.5	26.8	10.00	74.80	17.87	152.70	1454.79	344.19	H	Plantaginaceae

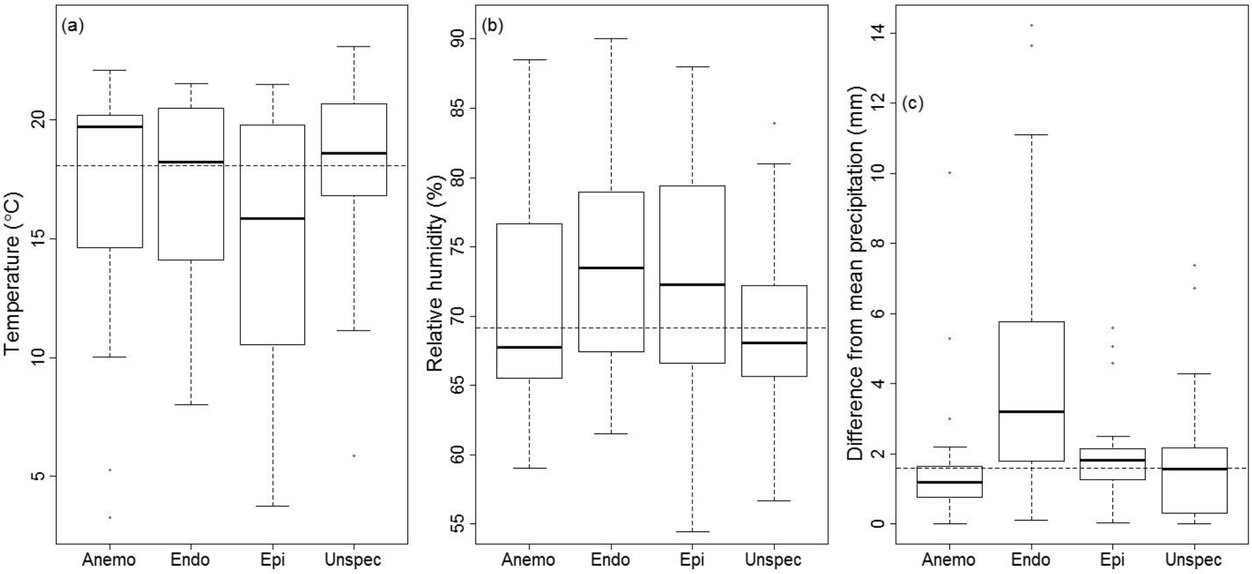

Figure i-A 1: Mean temperature, relative humidity, and precipitation (Figure a, b, and c, respectivley) during periods of diaspore release differentiated by the dispersal mode of the species. The dashed line shows the median of the respective variable during the entire period of diaspore release. For each plot, data for 104 species are shown (see Figure i-2 for number of species per dispersal mode).

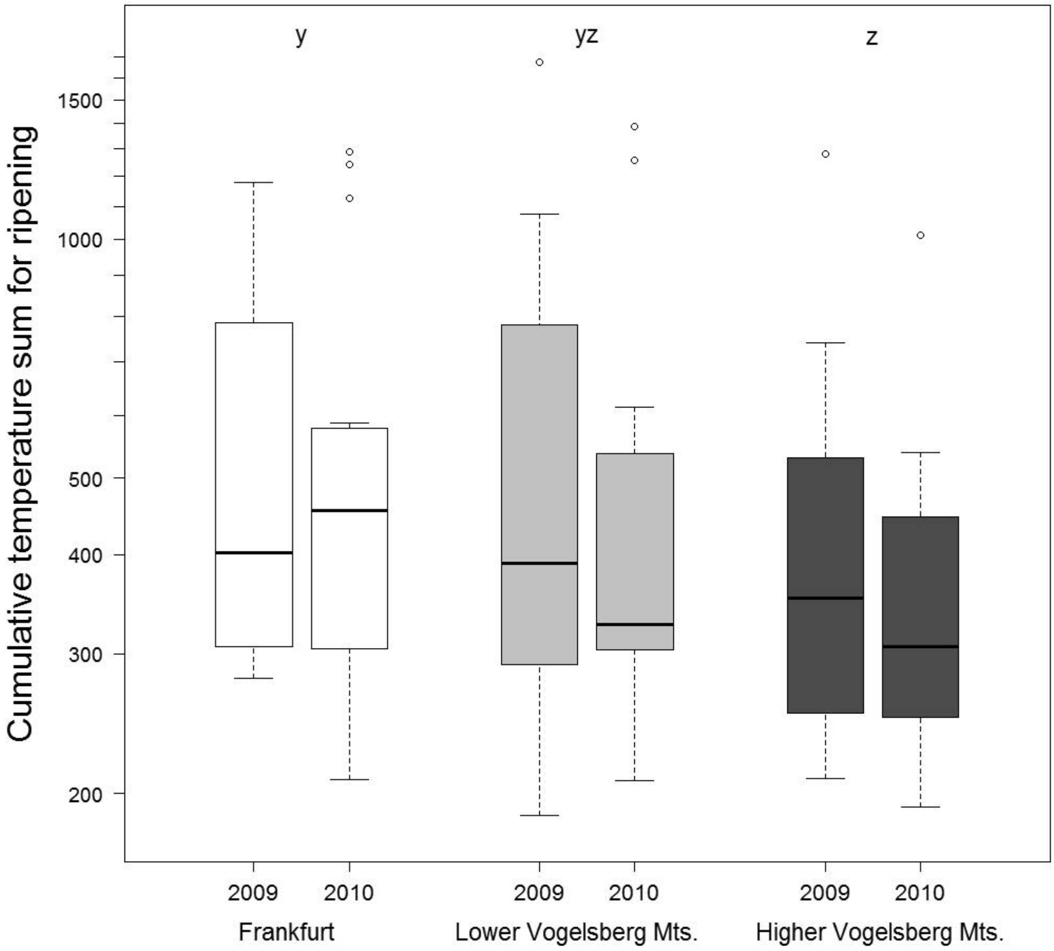

Figure i-A 2: Cumulative temperature sum for the duration of ripening for 18 species, differentiated by the three sites ‘Frankfurt’, ‘Lower Vogelsberg Mts.’ and ‘Higher Vogelsberg Mts.’ and two years ‘2009’ and ‘2010’.

8.2 Project ii: Seasonal synchronisation of seed release phenology promotes long-distance seed dispersal by wind for tree species with medium wind dispersal potential

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Erklärung zu den Autorenanteilen

an der Publikation: Seasonal synchronization of seed release phenology promotes long-distance seed dispersal by wind for tree species with medium wind dispersal potential.

Status (*submitted, under review, in revision, accepted*): accepted

Beteiligte Autoren:

- Felix Heydel (corresponding author) (FH, Promovierender)
- Sarah Cunze (SC)
- Markus Bernhardt Römermann (MBR)
- Oliver Tackenberg (OT, Betreuer)

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?

(1) zu Entwicklung und Planung

Promovierender: 65%

Co-Autor OT: 35%

(2) zur Durchführung der einzelnen Untersuchungen und Experimente

Promovierender: 90% FH führte die Computersimulationen sowie die Literaturrecherche zur Phänologie der Diasporen Ausstreu selbstständig durch
Co-Autor OT: 10% OT parametrisierte das Simulationsprogramm PAPPUS und brachte sich bei der Beschaffung phänologischer Daten zur Ausstreu von Offenlandarten ein

(3) zur Erstellung der Datensammlung und Abbildungen

Promovierender: 85% FH führte die Datenaggregierung, -aufbereitung und die Qualitätskontrolle durch. FH erstellte die Datengrundlage und Abbildungen für das oben genannte Manuskript.
Co-Autorin SC: 5% beriet bei der Berechnung der Migrationsraten
Co-Autor OT: 10% OT beriet die Abläufe der oben genannten Datenarbeiten.

(4) zur Analyse und Interpretation der Daten

Promovierender: 75% FH führte die Analysen durch.
Co-Autorin SC: 5% beriet bei der Durchführung der statistischen Analysen.
Co-Autor MBR: 10% MBR beriet bei der Durchführung der statistischen Analysen.
Co-Autor OT: 10% OT beriet bei der Durchführung der statistischen Analysen.

(5) zum Verfassendes Manuskripts

Promovierender: 80%
Co-Autorin SC: 5%
Co-Autor MBR: 5%
Co-Autor OT: 10%

8.2.1 Abstract

Questions: How does the seasonal variability of wind affect the seed release phenology of plant species from different vegetation types? Do wind-dispersed plant species show a seasonal synchronisation of seed release with meteorological conditions that promote long-distance dispersal (LDD) by wind?

Location: Germany, Central Europe

Methods: We combined empirical observations of seed release phenology with simulations of LDD by wind. We simulated LDD by wind for species differing in seed terminal velocity for open and forested habitats using a broad set of measured meteorological conditions. In order to investigate the extent of seasonal synchronisation of seed release with LDD, we compared species' LDD throughout the year with phenological data on timing of seed release for herbaceous species from open and tree species from forested habitats.

Results: For tree species with winged seeds and medium seed terminal velocity (e.g. *Acer platanoides*, *Tilia cordata*), we found a pronounced seasonal synchronisation of seed release timing with high LDD by wind. These species showed an extended ripening duration together with both the highest rate of seed release and high LDD in wintertime. Species with low seed terminal velocity (i.e. high wind dispersal potential) from open habitats (mainly species from the Asteraceae family with plumed seeds) and forested habitats (e.g. tree species of the genera *Populus*, *Salix*) both showed high LDD but lacked in seasonal synchronisation of seed release timing with LDD.

Conclusions: For forest species with medium seed terminal velocity, the seasonal timing of seed release during wintertime, exhibiting strong winds, could be evidence for phenological adaptations to timing of wind dispersal within periods with favourable conditions. Our finding that species with low seed terminal velocity and high LDD throughout the year did not show seasonal seed release synchronisation tentatively suggests that selection for other mechanisms such as synchronisation with short-term weather events might promote LDD of these species. Our results provide insights in how seasonal seed release timing of plant species from different vegetation types affects LDD by wind and shows that seed release phenology should be considered while assessing species' wind dispersal potential.

Keywords: anemochory; forest; open landscape; phenological adaptations; reproductive phenology; seasonal synchronization; vertical turbulence, wind speed, wind dispersal model; wind-dispersed species

8.2.2 Introduction

The phenology of plants is generally shaped by environmental conditions (Menzel et al. 2006), biological interactions (Vanschaik et al. 1993) and phylogenetic relations (Davies et al. 2013). Seed dispersal drives many important processes in plant ecology and evolution and has long-term consequences for spatiotemporal dynamics of plant species, communities, and ecosystems (Kawecki & Ebert 2004; Cunze et al. 2013; Maurer et al. 2013). The timing of seed release is important when estimating plant spread because of seasonality in the availability and strength of many dispersal vectors (Cousens et al. 2008). For example, the timing of seed release and dispersal may enhance the probability for seeds to meet favourable environmental conditions during e.g. establishment of seeds and offspring survival, thus functioning as a risk-reducing trait (Harper 1977; Kubitzki & Ziburski 1994; Hamann 2004; Öster et al. 2009). Besides the effects of seed release phenology on the environmental conditions during early life-cycle events, the seasonality in the availability of dispersal vectors may affect the distance travelled by the diaspore. However, despite its acknowledged importance, the effect of seed release phenology on dispersal distances has only rarely been investigated, particularly in regions affected by seasonality such as temperate habitats (e.g. Nathan & Katul 2005; Wright et al. 2008).

Seed dispersal and especially rare long-distance dispersal (LDD, Clark et al. 1998; Higgins et al. 2003) events primarily drive plant spread in space and time and thus strongly affect future plant diversity (Pitelka et al. 1997; Parmesan & Yohe 2003; Cunze et al. 2013). LDD is typically driven by large migratory animals, extreme meteorological weather conditions, ocean currents, and transport by humans (Nathan et al. 2008). Generally, the unpredictable occurrence of these extreme events has led to the traditional perception of LDD as a coincidental phenomenon (Carlquist 1981; Nathan et al. 2001), which may only be weakly affected by natural selection (Carlquist 1981; Berg 1983).

Recently, however, the idea that LDD could evolve through changes in phenological traits like the timing of seed maturity and seed release rather than in classically studied morphological traits has been challenged (Nathan et al. 2008). At the scale of meteorological short-time events, a synchronisation between timing of seed release and LDD is well known.

Seed abscission may, in fact, strongly be affected by environmental factors such as wind speed (Soons & Bullock 2008) and drying conditions for seeds rather than being simply due to maturation alone (Sharpe & Fields 1982; Greene & Johnson 1992). For instance, for preferential seed release during favourable periods for dispersal, specific morphological structures were recently suggested to enhance seed abscission during updrafts and to promote LDD by wind (Greene & Quesada 2011, Maurer et al. 2013). At the seasonal time scale, the timing of seed release is often suggested to be a result of selection for dispersal at the time in the year exhibiting optimal conditions for LDD by both wind and animals (e.g. Janzen 1967; Griz & I. C. S. Machado 2001; Hamann 2004; Du et al. 2009). Synchronisation of seed abscission with periods showing high wind speed is suggested as an effective plant-controlled mechanism increasing LDD in wind dispersed *Pinus halepensis* (Nathan et al. 2000) and *Tabebuia rosea* (Wright et al. 2008). Seasonality in seed dispersal may also correspond to seasonality in animal behaviour (e.g. Estrada & Coates-Estrada 2001; Hamann 2004) and positively affect dispersal distances.

Empirical evidence concerning the importance of timing of seed release and effects of dispersal seasonality on LDD is scarce, especially for species from temperate climates. For example, many of the above-mentioned studies address the effect of dispersal timing by focussing on only one or few species (e.g. Nathan et al. 2000; Wright et al. 2008; Maurer et al. 2013). Although the phenology of seed release at the seasonal time scale is considered as vitally important for the assessment of species' wind dispersal potential throughout the year and for opening new directions in the study of LDD evolution, it has only received minor attention until now.

The meteorological conditions that affect transport of seeds during wind dispersal closely depend on the structure of the vegetation type, topography, and landscape texture (Finnigan & Kaimal 1994). Within a vegetation type, the specific position of diaspores with respect to the canopy surface has an effect on LDD by wind (Detto et al. 2008). As such, plant individuals dispersing their seeds above the canopy are regarded as 'hot spots' of LDD by wind (Horn et al. 2001; Nathan & Katul 2005; Bohrer et al. 2008). For LDD by wind, trajectory simulation models provide good estimations of how far seeds are expected to disperse (Nathan et al. 2002) and therefore supply the most accurate results of plant spread (Kuparinen 2006, Nathan et al. 2011a). In mechanistic approaches of seed dispersal modelling, the seed aerodynamics and particularly the seed terminal velocity (V_{term}) during fall is often considered as the principal plant trait that affects LDD in wind-dispersed species (Green 1980; Nathan et al. 2001; Tackenberg 2003). Currently, the question of which particular wind conditions promote

LDD is under debate. Convective updrafts (Tackenberg et al. 2003b; Soons et al. 2004) and horizontal wind speed (Jongejans & Schippers 1999; Nathan et al. 1999; Nathan et al. 2002) were both proposed to play an important role. Recently, different vegetation types were suggested to show divergent interactions of species traits, updrafts, and horizontal wind speed that promote LDD by wind (Heydel et al. 2014).

In this study, we test the hypothesis that plant species that are adapted to wind dispersal release their seeds predominantly during periods with favourable conditions for LDD by wind. We aim to answer the following questions in particular: (i) Do wind-dispersed species show a seasonal synchronisation between the timing of seed release and LDD by wind? (ii) Which are the specific wind conditions that promote species' LDD in different vegetation types and seasons? (iii) Which species show higher potential migration rates? (iv) When do wind-dispersed plant species from different vegetation types release their seeds?

To answer these questions we combined modelled seed dispersal distances by wind with empirical observations of seed release phenology. We simulated LDD of seeds by wind based on a broad dataset of meteorological data from open and forested habitats from the temperate zone. In addition, data on the phenology of seed ripening and seed release for species from open forested habitats were gathered from literature. In order to assess the existence of phenological adaptations to LDD by wind, we compared this phenological data with the simulation of LDD and analysed the extent of seasonal synchronisation of seed release with meteorological conditions that promote LDD by wind.

8.2.3 Methods

8.2.3.1 Phenological data on seed ripening, release time, and terminal velocity

We gathered data on reproductive phenology for 125 Central European species from open habitats (Müller-Schneider 1986) and 40 Central European tree species from forested habitats (Schütt et al. 1995, see Table ii-A 1 on page 147) from literature. Duration of ripening was calculated as the period between onset of flowering (data from Jäger & Werner 1995) and onset of seed release. The above-mentioned comprehensive data on species' phenology consisted of monthly values for timing of events, which is why subsequent main analyses were conducted at this lowest common temporal resolution.

In order to classify the total of 165 study species with respect to their wind dispersal potential, we assigned the species into different V_{term} groups with thresholds (based on previous simulations, see Fig.4 in Tackenberg et al. 2003a) as follows: group "low" V_{term} (mainly species with plumed and winged seeds) with $V_{term} < 1$ m s^{-1}, group “medium” V_{term} (many species winged seeds) with 1 m s^{-1} <= V_{term} <= 2 m s^{-1} and group “high” V_{term} (species without obvious adaptations to wind dispersal) with $V_{term} > 2$ m s^{-1}. Data on V_{term} of the species were retrieved from Hintze et al. (2013) and own measurements. Species-specific data on V_{term}, timing of flowering and seed release are provided in Table ii-A 1.

8.2.3.2 Modelling seed dispersal by wind using PAPPUS

We simulated wind dispersal using PAPPUS, a mechanistic wind dispersal model that simulates trajectories of individual seeds (Tackenberg 2003). While analytical models are only able to predict mean dispersal distances, trajectory models consider the movement of particles within the airflow and are able to incorporate rare wind conditions driving LDD. Thus, trajectory models are preferable for modelling wind dispersal over short and long distances (Kuparinen 2006, Nathan et al. 2011a). PAPPUS was validated by comparing dispersal distance distributions generated by simulations with empirically observed distance spectra from release experiments in different landscapes and under various weather conditions (Tackenberg 2003).

Similar to most trajectory models, PAPPUS uses two species-specific traits: the initial release height and V_{term}. In the simulations, the flight of a seed is subdivided into periods of 0.1 s, and its movement is calculated separately for each period as a sum of the wind vector (horizontal wind speed, direction, and vertical wind speed) and V_{term}. The decrease of wind speed with declining height above ground is taken into account by a logarithmic vertical wind profile, which is regulated by the roughness of the vegetation cover (e.g. McCartney 1990) and was set to 0.1 for all study sites. In PAPPUS, the simulation stops once the seed falls below the closed vegetation canopy and transport over large distances only occurs while seeds are above the vegetation canopy (as also argued by Nathan et al. 2002).

The course of the wind vector during the flight of a seed is dynamic due to vertical and horizontal turbulence (Mazzoni 1996). In PAPPUS, the course of the wind vector is not modelled, but is derived from high-frequency measurements of the course of the wind vector (using ultrasonic anemometers) during a reference period (Tackenberg et al. 2003a). This empirical component allows realistic consideration of rare events, e.g. convective updrafts, which are an important determinant of LDD by wind in empirical studies (Tackenberg 2003, Bohrer et al. 2008) as well as in simulation studies (e.g. Tackenberg et al. 2003b). As with most trajectory models, PAPPUS does not consider the effect of release thresholds on LDD yet (Schippers & Jongejans 2005, but see Kuparinen 2006; Horn et al. 2012). The simulations performed with PAPPUS result in discrete dispersal events, which constitute discrete probability density functions of dispersal distances (i.e. dispersal kernel) when repeating simulations.

8.2.3.3 Traits of the model species

For each of both open and forested habitats, LDD was simulated for three different model species. For each vegetation type, the three species were fit to represent the V_{term} species groups mentioned in subsection 2.1. The three model species were characterised by three different V_{term} values = 0.4, 1.6 & 3.2 m s^{-1}, so that results can be transferred to a wide range of ‘real’ plant species. The initial height of seed release above the canopy was set to 0.4 m, as it has only minor effects on LDD compared to V_{term} (Heydel et al. 2014). Using ‘the initial height of seed release above the canopy’ instead of using ‘the height of seed release above ground’ implies that the seeds of species from both vegetation types have identical falling heights to the closed canopy. Therefore, the results for species' LDD are directly comparable between vegetation types even if they differ in height structure.

8.2.3.4 Simulation of dispersal kernels in different environments

The most important meteorological parameter affecting seed dispersal is the course of the wind vector (wind direction, vertical and horizontal wind speed) and its fluctuations, i.e.

turbulence. The two vegetation types analysed in this study were characterised by empirical wind data from two open habitat sites (arable land, grassland) and two forested habitat sites (spruce forests). The high-frequency measurements of the wind vector originate from the three years 2004 to 2006 (Table ii-A 2, further details described in Grünwald & Bernhofer 2007; Lehner 2008; Prescher et al. 2010). All data were assessed for quality and was processed to a temporal resolution of 10 Hz.

With available wind data, we calculated 200 trajectories with randomly chosen starting times per hour for each species, vegetation type, and site. Subsequently, we built weekly dispersal kernels by randomly choosing dispersal distances from the respective week. Weekly kernels that exhibited less than 30,000 trajectories (e.g. due to gaps in measurements) were excluded from the dataset. The proportion of available wind data were 53 %, 64 %, 69 % in the open habitats and 68 %, 77 %, 77 % in the forested habitats for the years 2004, 2005, and 2006, respectively. The dispersal simulations took place in flat landscapes without topographic features that were covered in continuous and homogenous vegetation of each type.

8.2.3.5 Migration rates as a measure of LDD

In order to generate a general measure of LDD we used migration rates as suggested by Clark et al. (2001), as they are mainly influenced by the tail of the species' dispersal kernel. For each week and for each species, migration rates (in m per year) were calculated from the dispersal kernels as the expected value of the maximum of a random sample of the size of the number of offspring at seed release (R_0), divided by the generation time (T, in years) following Clark et al. (2001) (see also Higgins et al. 2003). In order to generate a measure of LDD that is only sensitive to differences in seed characteristics of species (V_{term}) and the vegetation type, the two demographical parameters were constantly assumed with $R_0 = 100$ and T = 1. From the weekly migration rates, we calculated monthly median migration rates in order to gain insights into the course of migration rates throughout the year. Below, we will mostly refer to the median, as it is a more robust measure of central tendency than the mean. However, when interpreting the values of migration rates, it should be kept in mind that LDD and migration rates depend on rare events. Thus, our estimates of median migration rates are rather conservative and other measures, such as the mean, might be considerably higher (cf. Table ii-A 3). As most plant species release their seeds in a particular period in the year, only the calculated migration rates that lie within the actual dispersal period of the species are likely to be realised in nature. Hence, we rather refer to the term 'potential migration rates'.

8.2.3.6 Meteorological measures for updrafts and wind speed

In order to provide measures of the prevailing wind conditions for LDD, we calculated meteorological parameters for each week. First, we calculated *TURB* in 0.4 m height above the canopy as the proportion of LDD relevant updrafts, assuming a logarithmic vertical wind profile. *TURB* is a measure of the intensity of vertical turbulence in relation to the V_{term} of the species. It is calculated as the proportion of time, during which updrafts of a vertical wind speed that is greater than the V_{term} of the respective species occur (see Tackenberg 2003, Tackenberg et al. 2003b). This proportion of time for which the vertical wind speed was averaged is measured by dividing 100 m by the mean horizontal wind speed. Hence, updrafts of that strength and duration are capable of prolonging the flight of a seed to reach a distance of 100 m without losing altitude in relation to the initial release height. Second, we calculated *WIND* as the mean horizontal wind speed in 0.4 m height above the canopy. In order to ensure that *WIND* is sensitive to rare meteorological events, we tested for the relationship between *WIND* and an alternatively calculated measure of wind speed. We calculated *WIND'* as the weekly proportion of seconds that showed wind speeds greater than 4 m s^{-1}. The threshold of 4 m s^{-1} was chosen because the proportions of occurrence of these rare meteorological events were comparable for *WIND'* and *TURB*. The correlation between *WIND* and *WIND'* was highly significant for both vegetation types (GLM analysis with = $p < 0.001$, Table ii-A 4 on page 152). To provide an easily interpretable measure for wind speed, we used the variable *WIND* for subsequent analyses. In order to relate *TURB* and *WIND* data to the simulations for species' LDD, we calculated monthly mean values.

8.2.3.7 Statistical analysis

Differences in the timing of seed release between the V_{term} groups were analysed separately for each vegetation type. We created monthly distributions for seed release and used these to test for differences between species V_{term} groups by using the Kolmogorov-Smirnov test. Differences between the duration of seed release of species (grouped by their V_{term}) in both open and forested habitats were analysed using three different GLMs. Using a GLM we tested whether potential migration rates depend on V_{term}, vegetation type, and proportion of species releasing their seeds. Models were set up using the gamma error distribution family. Models were simplified using backward selection of the non-significant variables until the final minimal adequate model contained only significant terms (*p* value <0.05, Crawley 2007) and a minimal Akaike Information Criterion (AIC) was obtained (Crawley 2007). All statistical analyses were performed with R 3.1.3 (R Core Team 2015).

8.2.4 Results

8.2.4.1 The effect of species' Vterm and vegetation type on potential migration rates

In both vegetation types, species with low V_{term} generally showed higher potential migration rates than species with medium or high V_{term} (Figure ii-1). In both vegetation types, potential migration rates differed significantly between the V_{term} groups ($p < 0.001$, Table ii-A 5). Generally, high potential migration rates were found for forest species with low and medium V_{term} (median potential migration rate = 2160 and 46 m yr^{-1}, respectively) as well as for species from open habitats with low V_{term} (median potential migration rate = 27 m yr^{-1},Figure ii-1). Low potential migration rates were found for species from open habitats with medium and high V_{term} (median potential migration rate = 1.2 and 0.5 m yr^{-1}, respectively) as well as for forest species with high V_{term} (median potential migration rate = 1.1 m yr^{-1}). In the analyses outlined below, we will focus on forest species with low and medium V_{term} and on species from open habitats with low V_{term}, for which wind dispersal seems to have an effect on LDD. Please note that we here provide only monthly medians of the potential migration rates and that other measures (see Table ii-A 3) and other averaging periods may result in much higher migration rates.

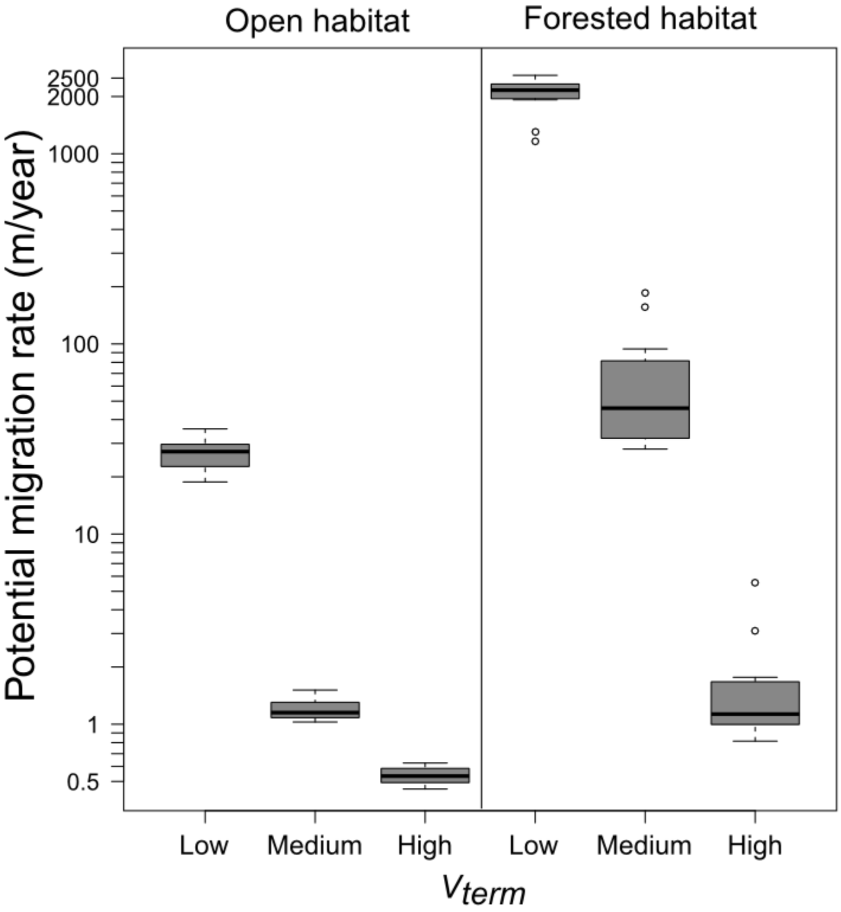

Figure ii-1: Potential migration rates for open and forested habitats and three species groups differing in seed terminal velocity. Each box plot represents 12 potential migration rates for each month of the year (averaged over three years). Within each vegetation type, the potential migration rates differed between each *Vterm* group (generalised linear model analysis, Table ii-A 5). Potential migration rate is shown on a log-scaled axis.

8.2.4.2 Within-year variability in potential migration rates, TURB and WIND

For species from open habitats with low V_{term}, within-year differences in potential migration rates were small and less than 20 m yr^{-1} (Figure ii-2a). For these species, potential migration rates were twice as great in August compared to June. Likewise, mean *TURB* (a measure of the intensity of vertical turbulence in relation to the V_{term} of the species) was more than 20 times greater in August than in June (Table ii-1) while mean *WIND* was even smaller in August than in June. For forest species with low V_{term}, potential migration rates were high from spring until the beginning of autumn (Figure ii-2d). For these species, potential migration rates were twice as high in July than in November (absolute differences in potential migration rates = 1402.6 m yr^{-1}). Interestingly, *TURB* was about 20 % higher in July than in November whereas *WIND* was about 30 % lower in July (Table ii-1). For forest species with medium V_{term}, potential migration rates were highest in February and more than six times higher than in June or December (absolute differences in median potential migration rates = 157.8 and 160.6 m yr^{-1}, respectively). Even if median migration rates were very low in December, the mean migration rates were stable throughout wintertime, which indicates that the LDD events were less frequent in December. For forest species with medium V_{term}, *TURB* was more than 170 times greater in January than in June, while *WIND* was only 30 % greater in January.

8.2.4.3 Timing of seed release

For species from open habitats, timing of seed release mainly occurred from summer until autumn (Figure ii-2a) and was not significantly different between species' V_{term} (according to the Kolmogorov-Smirnov test). For forest species, timing of seed release was significantly different between low and high V_{term} (Kolmogorov-Smirnov test statistic = 0.4, $p < 0.01$). Seed release of forest species with low V_{term} was relatively equal across all months of the year (Figure ii-2d). In May and June, nearly 40 % of the species with low V_{term} released their seeds (particularly species from the genera *Populus* and *Salix*, Figure ii-2). For forest species with medium V_{term}, 90 % of the species released their seeds during autumn and winter.

Table ii-1: Summary table of meteorological parameters *TURB* and *WIND*. *TURB* is a measure of the intensity of vertical turbulence in relation to seed terminal velocity (V_{term}) of the species (Tackenberg 2003). Letters indicate V_{term} groups (L, low; M, medium; H, high). *WIND* (horizontal wind speed) is not differentiated by V_{term}.

		Open habitat								**Forested habitat**							
		TURB						**WIND (m s^{-1})**		**TURB**						**WIND (m s^{-1})**	
		V_{term}_L		V_{term}_M		V_{term}_H		--		V_{term}_L		V_{term}_M		V_{term}_H		--	
Month	Season	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	Winter	0.001	0.002	<0.001	<0.001	<0.001	<0.001	1.567	0.662	0.241	0.084	0.010	0.016	0.001	0.002	1.888	0.385
2	Winter	0.001	0.002	<0.001	0.001	<0.001	0.001	1.532	0.724	0.230	0.110	0.018	0.032	0.001	0.001	1.713	0.367
3	Spring	0.002	0.003	<0.001	<0.001	<0.001	<0.001	1.447	0.352	0.194	0.091	0.002	0.004	<0.001	<0.001	1.629	0.321
4	Spring	0.054	0.120	<0.001	<0.001	<0.001	<0.001	1.341	0.626	0.144	0.093	<0.001	0.001	<0.001	<0.001	1.366	0.176
5	Spring	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.224	0.249	0.156	0.092	0.001	0.001	<0.001	<0.001	1.518	0.189
6	Summer	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.126	0.268	0.112	0.042	<0.001	<0.001	<0.001	<0.001	1.454	0.181
7	Summer	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	0.975	0.211	0.141	0.062	<0.001	0.001	<0.001	<0.001	1.362	0.216
8	Summer	0.002	0.004	<0.001	<0.001	<0.001	<0.001	1.041	0.174	0.117	0.072	<0.001	<0.001	<0.001	<0.001	1.496	0.161
9	Autumn	0.010	0.034	<0.001	<0.001	<0.001	<0.001	1.033	0.303	0.167	0.076	<0.001	0.001	<0.001	<0.001	1.529	0.221
10	Autumn	0.001	0.003	<0.001	<0.001	<0.001	<0.001	1.122	0.278	0.173	0.082	<0.001	0.001	<0.001	<0.001	1.612	0.190
11	Autumn	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.493	0.457	0.117	0.056	0.001	0.002	<0.001	<0.001	1.866	0.332
12	Winter	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.473	0.387	0.097	0.055	0.001	0.001	<0.001	<0.001	1.830	0.348
	Seasonal mean values																
	Winter	0.001	0.002	<0.001	0.001	<0.001	0.001	1.521	0.559	0.189	0.105	0.010	0.022	0.001	0.001	1.789	0.358
	Spring	0.018	0.071	<0.001	<0.001	<0.001	<0.001	1.335	0.438	0.167	0.094	0.001	0.002	<0.001	<0.001	1.513	0.267
	Summer	0.001	0.002	<0.001	<0.001	<0.001	<0.001	1.044	0.222	0.123	0.060	<0.001	<0.001	<0.001	<0.001	1.439	0.191
	Autumn	0.004	0.021	<0.001	<0.001	<0.001	<0.001	1.177	0.376	0.151	0.074	<0.001	0.001	<0.001	<0.001	1.676	0.293

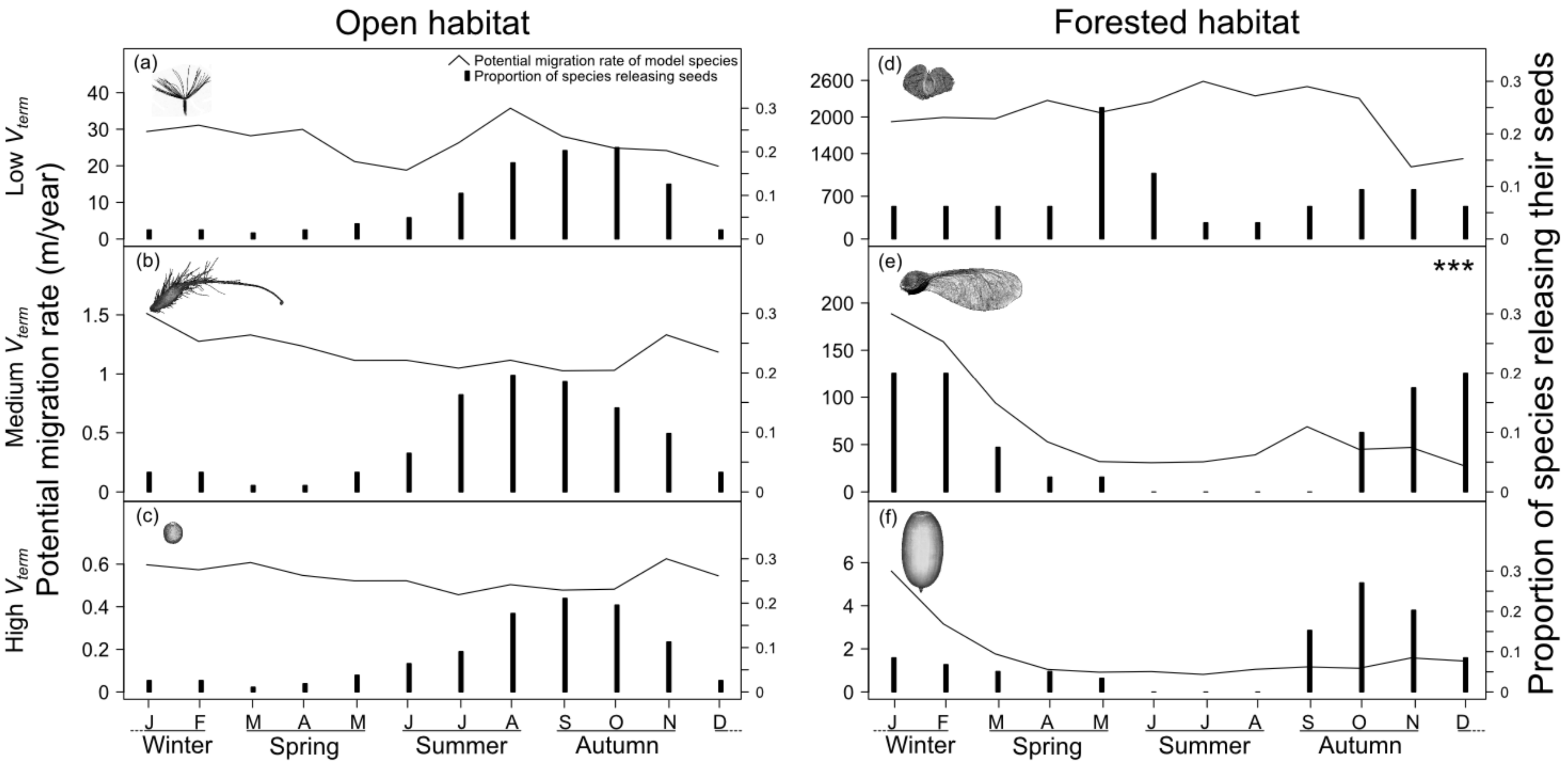

Figure ii-2: Potential migration rates and proportion of species releasing their seeds for species from open (a - c) and forested habitats (d - f) for each month of the year. For both vegetation types data are shown for low (a, d), medium (b, e) and high seed terminal velocity (Vterm) (c, f). The effect of the proportion of species releasing their seeds on the potential migration rates was significant only for forest species with medium Vterm ($p < 0.01$, Table ii-A 5). In the open habitat, the number of species was 41, 35 and 49 for low, medium and high Vterm, respectively. In the forested habitat, the number of species was 13, 10 and 17 for low, medium and high Vterm, respectively. Images within each plot exemplarily demonstrate seed morphology for each Vterm group and show *Eupatorium cannabinum L.* (a), *Geum rivale L.* (b), *Salvia pratensis L.* (c), *Betula pendula Roth* (d), *Acer pseudoplatanus L.* (e) and *Quercus robur L.* (f).

8.2.4.4 Duration of phenological phases

For species from open habitats with low V_{term}, ripening duration was significantly shorter compared to other species' V_{term} from both vegetation types (Table ii-2, Figure ii-3). For forest species with medium V_{term}, the duration of ripening was significantly longer than for species from open habitats, and forest species with low V_{term}. The seed release duration of forest species with low V_{term} was about two months and significantly shorter than seed release duration of all other species from both vegetation types.

Table ii-2: Summary statistics of the generalized linear model on the duration of ripening and seed release grouped by seed terminal velocity (Vterm) of the species. The model was based on phenological data of 125 and 40 species from open and forested habitats, respectively. The table includes estimates, standard errors (Std. Error), t- and corresponding p values for all significant interactions and variables. The model coefficients of a generalised linear model (GLM) using the gamma error distribution family can more easily be interpreted if the coefficient (e.g. estimate) is transformed into its reciprocal. Different symbols indicate significant differences from gamma distribution with ***$p < 0.001$ and **$p < 0.01$. Abbreviations: The first letter refers to open (O) and forested (F) habitats and the second letter refers to Vterm (L = low; M = medium; H = high).

	Estimate	**Std. Error**	***t* value**	***p* value**	
Seed ripening					
OL	0,422	0,026	16,091	<0.001	***
OH OM	–0.083	0,029	–2.844	0,005	**
FH FM	–0.275	0,028	–9.754	<0.001	***
FL	–0.201	0,034	–5.833	<0.001	***
Seed release					
OL OM OH FM FH	0,254	0,01	26,342	<0.001	***
FL	0,152	0,054	2,845	0,005	**

8.2.4.5 Seasonal synchronisation of potential migration rates and the proportion of species releasing their seeds

For forest species with medium V_{term}, we found a significant seasonal synchronisation (Figure ii-2e, GLM analysis for the effect of the proportion of species releasing their seeds on the potential migration rates = $p < 0.002$, Table ii-A 5). By contrast, the other V_{term} groups from both vegetation types showed no effect of the proportion of species releasing their seeds on potential migration rates.

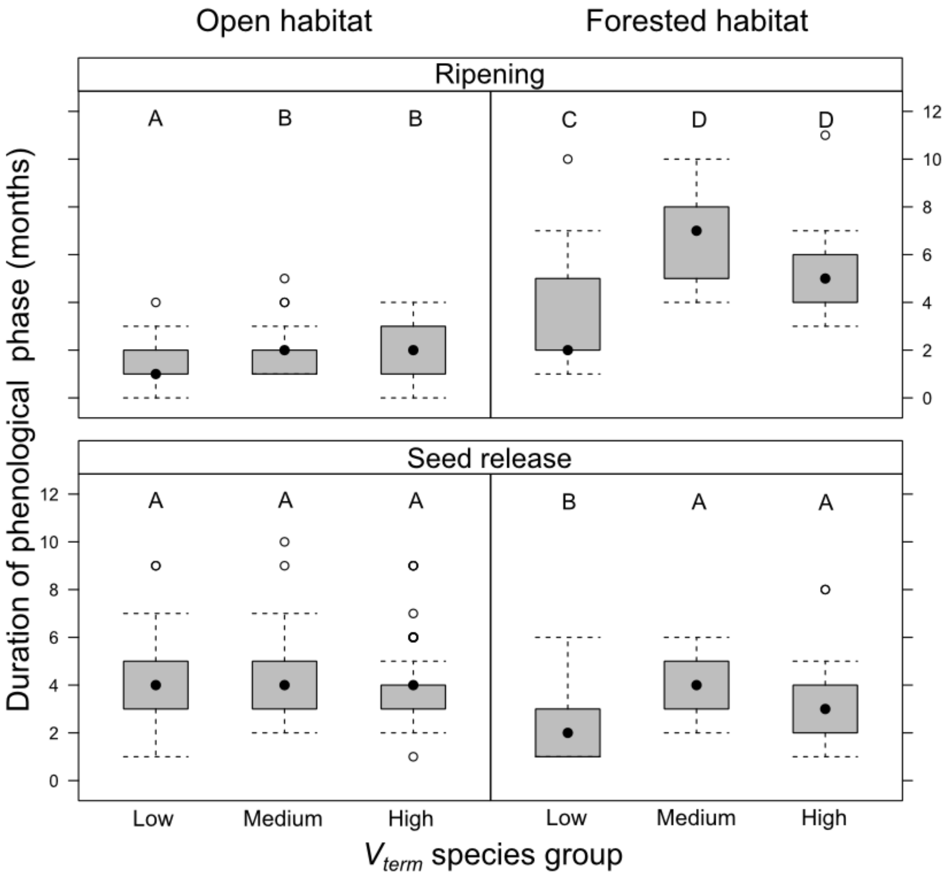

Figure ii-3: Duration of the phenological phases ripening and seed release for species from open and forested habitats. Species are grouped by their seed terminal velocity (Vterm). For the number of species from open and forested habitats in each Vterm group see Figure ii-2. For each phenological phase, different letters indicate significant differences between Vterm levels (see Table ii-2 for summary table of the generalised linear model analysis).

8.2.5 Discussion

In order to gain insights into how the seasonal variability of wind does affect the seed release phenology of plant species from different vegetation types, we analysed the amount of seasonal synchronisation of seed release with LDD (in terms of migration rates). For LDD by wind, Heydel et al. (2014) showed that migration rates are highly correlated to another measure of LDD, which refers to a pre-determined dispersal distance of 100 m, and can thus be used as a general measure of LDD.

8.2.5.1 Seasonal synchronisation of seed release and LDD by wind

Forest species with medium V_{term} (mainly species with winged seeds, e.g. *Abies alba*, *Acer platanoides*, *Carpinus betulus*, and *Tilia cordata*) showed a pronounced seasonal synchronisation of LDD with timing of seed release (Figure ii-2e). The seasonality of seed release had a highly significant effect on LDD for these species (GLM analysis in Table ii-A 5). Forest species with medium V_{term} showed both high LDD and the highest proportion of species releasing their seeds in winter. Higher LDD in winter than in summer was accompanied with both higher *TURB* and *WIND* in winter (Table ii-1, see also Hofherr & Kunz 2010) indicating that both parameters promote LDD of forest species with higher V_{term} (Heydel et al. 2014). For forest species with medium V_{term}, the pronounced seasonal synchronisation of seed release with higher LDD combined with a remarkably long ripening period is a tentative evidence of the existence of phenological adaptations to dispersal by wind for these species. Synchronisation of seed release with periods showing strong winds was suggested as a vital and effective plant-controlled mechanism to promote LDD of the wind-dispersed Mediterranean *Pinus halepensis* (Nathan et al. 2000). The matching of periods of optimal conditions for LDD by wind with timing of seed release was also found by Griz & I. C. S. Machado (2001) and Du et al. (2009). In addition, Hamann (2004) found dispersal periods of wind-dispersed species to be extended and thereby to match periods exhibiting with high wind speeds that are favourable for LDD by wind.

Forest species with low V_{term} (mainly species of the genera *Populus*, *Salix*, *Betula,* and *Ulmus*) showed both ongoing seed release and high potential migration rates throughout the year (Figure ii-2d). For these species, highest LDD in summer was associated with higher *TURB* and lower *WIND* than in late autumn (Table ii-1). This supports the finding that updrafts promote LDD of forest species with low V_{term} (Heydel et al. 2014). Apparently, their low V_{term} allows uplifting of seeds and considerable LDD in each month of the year. In accordance with our results, LDD was even high when wind velocity was low for the low V_{term} tropical tree *Jacaranda copaia* (Wright et al. 2008). Besides a seasonal synchronisation of seed release and LDD, for forest species with low V_{term} a short-term synchronisation of seed release with favourable conditions for LDD by wind seems likely. During dry periods, rapidly developing abscission layers of *Acer saccharinum* seeds (with low $V_{term} = 0.9$ m s^{-1}) were regarded as a mechanism for short-term synchronisation of seed release with LDD (Greene & Johnson 1992). Likewise, for the tropical tree *Luehea seemannii* with low $V_{term} = 0.7$ m s^{-1} preferential seed abscission during updrafts were found to promote LDD by wind (Maurer et al. 2013).

In the open habitats, species with low V_{term} (many species with plumed seeds from the Asteraceae family and species with winged seeds from the Poaceae family), which are clearly adapted to dispersal by wind, revealed only low differences in monthly potential migration rates (Figure ii-2a). When examined over the course of the year, these species showed no obvious seasonal synchronisation of seed release and LDD, which tentatively suggests that selection for other mechanisms such as synchronisation with short-term weather events might promote LDD of low V_{term} species from open habitats (see similar argument for low V_{term} species from forested habitats). Evidence for morphological mechanisms promoting the number of seed releases during high wind speed events was provided for two *Carduus* species (Jongejans et al. 2007) as well as for *Calluna vulgaris* and *Erica cinerea* (Soons & Bullock 2008). LDD of these species increased during turbulent conditions with low air humidity (see also Schippers & Jongejans 2005). As a further example of a short-term synchronisation of seed release with LDD, the capitulum of *Tragopogon dubius* was recently suggested to provide a morphological mechanism for updraft-selective release of seeds (Greene & Quesada 2011). For low V_{term} species from open habitats, we found that higher LDD was accompanied with higher *TURB* and lower *WIND*, which indicates an important role of *TURB* for LDD of such species (Tackenberg et al. 2003; Soons et al. 2004; Heydel et al. 2014).

The results found depend strongly on the temporal focus and resolution of our study, as we focused on phenological adaptations on a seasonal scale. Additionally, particular meteorological short-time events like e.g. dry air during calm periods or high wind speeds in gusts are commonly suggested to promote LDD by wind, especially for species with low V_{term} (Greene 2005). Hence, especially for species with low V_{term}, such short-time synchronisation might be much more important than a seasonal synchronisation.

8.2.5.2 Which species show higher potential migration rates?

Generally, we found higher potential migration rates for the forested than for the open habitats (Figure ii-1, Table ii-A 5). In the forested habitats, we found high potential migration rates for species with low V_{term} and medium V_{term}. In the open habitats, we found high potential migration rates for species with low V_{term}. For the mentioned species, we suggest that wind plays an important role for LDD.

By contrast, we found low potential migration rates for species from open habitats with medium and high V_{term} as well as for forest species with high V_{term} (Figure ii-1). While considering maximal instead of median values, species showed much higher potential migration rates (compare Table ii-A 3). Hence, dispersal by wind possibly could still be ecologically relevant for some species of the three mentioned V_{term} groups, particularly during (shorter) periods that may exhibit conditions more favourable for dispersal.

8.2.5.3 When do wind-dispersed species release their seeds?

Species from open habitats showed simultaneous timing of seed release that occurred mainly in autumn (Figure ii-2). This pattern of uniform seed release timing in species from open habitats with different V_{term} can be explained with environmental constraints of the end of the growing season on the development and reproduction of herbaceous plants. In contrast to woody species, aboveground plant material of herbaceous plants mostly withers in winter and is probably covered by snow. Hence, herbaceous species are climatically constrained to complete the actual life cycle event within the growing season (e.g. production of shoots and seeds, see also Ollerton & Lack 1992), and are therefore forced to release their seeds as long as the stem is intact and in upright position.

Forest species with low V_{term} showed altogether the shortest seed release duration (Figure ii-3). This result is in accordance with short seed release periods of wind-dispersed species with low V_{term} (Hamann 2004). Short seed release duration of forest species with low V_{term} might be related to short seed longevity of species from the genera *Populus* (Schütt et al. 1995; Gage & Cooper 2005) and *Salix* (Raven 1992). By contrast, forest species with medium V_{term} mainly dispersed in winter (Figure ii-2) and showed a remarkably long ripening period (Figure ii-3). For forest species with low and medium V_{term}, the diverging phenological patterns for the duration of ripening and seed release open up questions on the potential underlying evolutionary mechanisms. The stem of tree species is stable even throughout wintertime and this physical stability might play a considerable role in facilitating natural selection to shape the seed release phenology of woody plants. For the direct survival of trees, the vegetative phenology (e.g. leaf unfolding) is highly constrained by physiological, and seasonal constraints (Janzen 1971). As the reproductive phenology (e.g. seed production and release) is less strongly environmentally constrained, it could potentially be more easily shaped by natural selection than the vegetative phenology. Thus, the combination of the physical stability of woody plants together with the environmentally less strongly constrained seed release phenology possibly enables natural selection to shape the phenology of seed release.

8.2.5.4 Conclusions and outlook

In the interest of revealing broad community-wide patterns of the phenology of seed release, we provide an evaluation of the amount of seasonal synchronisation of seed release with LDD by wind for plant species from open and forested habitats. Tree species with medium V_{term} (e.g. from the genera *Abies, Acer, Fraxinus, Larix*) that are both ecologically and economically important showed a pronounced seasonal synchronisation of seed release with LDD by wind. The seasonal synchronisation for tree species with medium V_{term} could cautiously be regarded as an evidence for the existence of phenological adaptations to dispersal by wind. On the other hand, in both vegetation types, species with low V_{term} showed no seasonal synchronisation of seed release with LDD by wind. This lack of seasonal synchronisation is possibly due to a distinct synchronisation with meteorological short-time events like e.g. low humidity. To investigate the role of such short-time synchronisation, much shorter averaging times of simulation data as well as short-time phenological monitoring data should be considered in subsequent studies (cf. Greene 2005). Future directions of phenology research should not only look towards evidence for evolutionary adaptations, but also address questions related to potential interactions with climate change. Climate change driven enhancements of fruiting phenology (Menzel et al. 2006, Nathan et al. 2011b) could eventually lead to earlier seed release and could thereby possibly decrease the amount of seasonal synchronisation of seed release with LDD, particularly for seasonally synchronised forest species with medium V_{term}. Hence, species from forested habitats with medium V_{term} and strong seasonal synchronisation (e.g. species of the genera *Abies*, *Acer*, *Pinus*, *Fraxinus,* and *Tilia*) might experience decreases in LDD by wind. Especially for forest species, habitat fragmentation and changes in landscape heterogeneity due to altered land use patterns are likely to affect microclimatic conditions and should be considered in future studies. Our findings provide insights in evolutionary processes that drive the optimisation of the timing of seed release and suggest that the dispersal phenology should be considered while assessing species' wind dispersal potential throughout the year.

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8.2.7 References

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8.2.8 Supplementary material

Table ii-A 1. Data on seed terminal velocity (V_{term}) and phenology of Central European plant species from open and forested habitats. V_{term} species groups were classified according to the V_{term} of species with V_{term}-low = 1 m s^{-1} <= V_{term}-medium <= V_{term}-high 2 m s^{-1}. F.B. = beginning of flowering, F.E. = end of flowering, S.B. = beginning of seed release, S.E. = end of seed release. Data on V_{term} were obtained from Hintze et al. (2013). For V_{term} values labelled with a star, V_{term} was not available for the particular species and was obtained as a mean of the respective genus. For cited literature on phenology see the box below this table.

Species name	***V_{term}* [m/s]**	***V_{term}* group**	**F.B.**	**F.E.**	**S.B.**	**S.E.**	**Data source for phenology**
Species from open habitats							
Agrostis capillaris L.	0.89	low	6	7	8	5	1
Apera spica-venti (L.) P. Beauv.	0.97	low	6	7	7	10	1
Arnica montana L.	0.83	low	6	7	8	10	1
Calamagrostis epigejos (L.) Roth	0.18	low	7	8	7	10	1
Carduus crispus L.	0.43	low	7	9	8	10	1
Carduus nutans L.	0.48	low	7	9	10	10	1
Carlina acaulis L.	0.72	low	7	9	9	11	1
Carlina vulgaris agg.	0.55	low	7	9	8	11	1
Chondrilla juncea L.	0.42	low	7	9	7	10	1
Cirsium arvense (L.) Scop.	0.26	low	7	9	7	11	1
Cirsium eriophorum (L.) Scop.	0.62	low	7	9	9	10	1
Cirsium palustre (L.) Scop.	0.36	low	7	9	8	10	1
Cirsium vulgare (Savi) Ten.	0.29	low	6	9	8	11	1
Crepis biennis L.	0.52	low	5	8	5	9	1
Epilobium hirsutum L.	0.19	low	6	9	8	10	1
Erigeron acris L.	0.21	low	6	9	7	11	1
Eupatorium cannabinum L.	0.31	low	7	9	9	11	1
Gentiana asclepiadea L.	0.86	low	7	9	9	2	1
Hieracium aurantiacum L.	0.32	low	6	8	8	10	1
Hieracium pilosella L.	0.45	low	5	10	6	8	1
Hypochaeris radicata L.	0.52	low	6	9	7	10	1
Inula salicina L.	0.23	low	6	10	10	11	1
Jasione montana L.	0.95	low	6	8	9	10	1
Leontodon autumnalis L.	0.87	low	7	9	8	11	1
Leontodon hispidus L.	0.99	low	6	10	7	11	1
Linaria vulgaris Mill.	0.94	low	6	10	8	11	1
Mycelis muralis (L.) Dumort.	0.36	low	7	8	7	10	1
Pulicaria dysenterica (L.) Bernh.	0.37	low	7	9	10	11	1
Saxifraga tridactylites L.	0.89	low	4	6	5	6	1
Senecio erucifolius L.	0.31	low	7	9	9	11	1
Senecio vulgaris L.	0.31	low	2	11	3	11	1
Solidago canadensis L.	0.32	low	8	10	9	11	1

Species name	V_{term} [m/s]	V_{term} group	**F.B.**	**F.E.**	**S.B.**	**S.E.**	**Data source for phenology**
Solidago virgaurea L.	0.52	low	7	10	9	5	1
Sonchus arvensis L.	0.24	low	7	10	7	11	1
Sonchus oleraceus L.	0.33	low	6	10	6	11	1
Teucrium chamaedrys L.	0.49	low	7	8	9	5	1
Tragopogon dubius Scop.	0.38	low	5	7	6	9	1
Trisetum flavescens (L.) P. Beauv.	0.78	low	5	6	7	10	1
Tussilago farfara L.	0.17	low	3	4	4	7	1
Valeriana officinalis agg.	0.40	low	5	8	8	10	1
Vincetoxicum hirundinaria Medik.	0.60	low	5	8	8	2	1
Achillea millefolium L.	1.36	medium	6	10	8	11	1
Arabidopsis thaliana (L.) Heynh.	1.19	medium	4	5	4	7	1
Briza media L.	1.69	medium	5	6	10	11	1
Bromus tectorum L.	1.96	medium	5	6	6	10	1
Buphthalmum salicifolium L.	1.95	medium	6	9	8	11	1
Calluna vulgaris (L.) Hull	1.08	medium	8	10	9	5	1
Campanula glomerata L.	1.93	medium	6	9	9	10	1
Campanula rotundifolia agg.	1.64	medium	6	10	8	10	1
Capsella bursa-pastoris (L.) Medik.	1.97	medium	1	12	5	10	1
Cardamine pratensis agg.	1.93	medium	4	6	6	7	1
Dactylis glomerata agg.	1.53	medium	5	7	6	2	1
Daucus carota L.	1.45	medium	6	9	8	2	1
Descurainia sophia (L.) Prantl	1.83	medium	5	9	8	11	1
Festuca ovina agg.	1.59	medium	5	8	6	8	1
Festuca rupicola Heuff.	1.36	medium	5	7	7	8	1
Filipendula ulmaria (L.) Maxim.	1.73	medium	6	8	10	2	1
Gentiana lutea L.	1.62	medium	6	8	9	2	1
Geum rivale L.	1.79	medium	4	7	8	10	1
Helictotrichon pratense (L.) Besser	1.10	medium	5	6	7	8	1
Helictotrichon pubescens (Huds.) Pilg.	1.76	medium	5	6	6	9	1
Heracleum sphondylium L.	1.89	medium	6	9	8	10	1
Holcus lanatus L.	1.18	medium	6	8	7	11	1
Holosteum umbellatum L.	1.60	medium	3	5	4	5	1
Linum catharticum L.	1.82	medium	6	7	7	11	1
Linum tenuifolium L.	1.52	medium	6	7	7	9	1
Molinia caerulea agg.	1.49	medium	7	9	9	11	1
Myosurus minimus L.	1.57	medium	4	6	7	9	1
Poa compressa L.	1.27	medium	6	7	7	11	1
Poa pratensis agg.	1.59	medium	5	6	6	9	1
Pulsatilla vulgaris s.l. Mill.	1.55	medium	4	5	5	8	1
Rhinanthus minor L.	1.50	medium	5	9	6	8	1
Scabiosa columbaria L.	2.00	medium	7	11	8	11	1
Stipa capillata L.	1.84	medium	7	8	8	2	1
Valeriana dioica L.	1.13	medium	5	6	8	9	1
Veronica arvensis L.	1.68	medium	3	10	5	8	1

Species name	V_{term} **[m/s]**	V_{term} **group**	**F.B.**	**F.E.**	**S.B.**	**S.E.**	**Data source for phenology**
Anthriscus sylvestris (L.) Hoffm.	4.72	high	5	8	6	8	1
Artemisia campestris L.	2.35	high	8	10	8	11	1
Artemisia vulgaris L.	2.04	high	7	11	9	11	1
Asperula cynanchica L.	6.45	high	6	9	8	10	1
Bromus erectus agg.	2.92	high	5	10	6	11	1
Bromus hordeaceus L.	2.17	high	5	8	6	9	1
Bromus inermis Leyss.	3.20	high	6	7	7	10	1
Bromus sterilis L.	2.37	high	5	6	6	8	1
Camelina microcarpa Andrz.	2.23	high	5	7	5	10	1
Carex montana L.	2.16	high	3	5	6	7	1
Cerastium holosteoides Fr.	2.48	high	3	6	5	10	1
Chenopodium album L.	3.37	high	7	10	8	10	1
Chenopodium polyspermum L.	3.79	high	7	9	8	10	1
Cichorium intybus L.	2.92	high	7	10	8	11	1
Danthonia decumbens (L.) DC.	2.59	high	6	7	7	9	1
Dianthus carthusianorum L.	2.38	high	6	9	9	11	1
Dipsacus fullonum L.	2.56	high	7	8	9	10	1
Echium vulgare L.	2.86	high	5	7	8	10	1
Festuca rubra L.	2.10	high	6	7	7	9	1
Galium verum agg.	3.27	high	6	9	8	10	1
Gentiana cruciata L.	2.01	high	7	8	9	11	1
Gentianella germanica (Willd.) Börner	3.30	high	6	10	9	5	1
Helianthemum nummularium s.l. (L.) Mill.	3.88	high	6	10	8	10	1
Hippocrepis comosa L.	3.50	high	5	7	8	11	1
Leucanthemum vulgare agg.	2.58	high	6	10	7	10	1
Lotus corniculatus L.	5.36	high	6	8	7	10	1
Medicago lupulina L.	3.80	high	5	10	8	11	1
Myosotis stricta Link ex Roem. & Schult.	3.01	high	3	6	5	7	1
Onobrychis viciifolia Scop.	2.36	high	5	7	8	11	1
Ononis repens L.	2.52	high	6	7	9	11	1
Pimpinella saxifraga L.	2.47	high	7	9	9	11	1
Plantago major s.l. L.	2.49	high	6	10	8	11	1
Poa annua L.	2.55	high	1	12	5	11	1
Primula veris L.	2.42	high	4	6	7	11	1
Prunella grandiflora (L.) Scholler	2.20	high	6	8	8	11	1
Prunella vulgaris L.	3.65	high	6	9	8	11	1
Ranunculus bulbosus L.	2.33	high	5	7	6	8	1
Salvia pratensis L.	2.55	high	5	8	6	9	1
Sanguisorba minor s.l. Scop.	2.83	high	5	8	7	10	1
Sanguisorba officinalis L.	3.52	high	6	9	9	2	1
Scleranthus annuus agg.	3.47	high	4	10	6	11	1
Scleranthus perennis L.	2.34	high	5	9	8	8	1
Silene otites (L.) Wibel	2.19	high	5	8	8	9	1
Stachys recta L.	2.20	high	6	10	8	11	1

Species name	V_{term} **[m/s]**		V_{term} **group**	**F.B.**	**F.E.**	**S.B.**	**S.E.**	**Data source for phenology**
Succisa pratensis Moench	2.32		high	7	9	9	11	1
Teucrium montanum L.	2.21		high	7	9	9	10	1
Thlaspi arvense L.	2.45		high	4	8	7	10	1
Trifolium pratense L.	3.65		high	6	9	8	10	1
Trifolium repens L.	2.62		high	5	9	8	10	1
Species from forested habitats								
Acer negundo L.	0.88		low	4	4	10	2	2
Betula pendula Roth	0.40		low	4	5	8	11	2
Betula pubescens Ehrh. s.l.	0.64		low	4	5	9	10	2
Picea abies (L.) H. Karst.	0.57		low	4	6	11	4	2
Pinus nigra J. F. Arnold	0.81		low	5	6	3	5	2
Populus alba L.	0.11	*	low	3	4	5	5	2
Populus nigra L.	0.11	*	low	4	4	5	5	2
Populus tremula L.	0.11		low	3	4	5	5	2
Salix alba agg.	0.56	*	low	4	5	5	6	2
Salix caprea L.	0.56	*	low	3	4	5	6	2
Salix fragilis agg.	0.56	*	low	3	5	5	6	2
Ulmus glabra Huds.	0.90	*	low	3	4	6	7	3
Ulmus laevis Pall.	0.90	*	low	3	4	5	5	2
Abies alba Mill.	1.06		medium	5	6	12	2	2
Acer campestre L.	1.21		medium	5	6	10	2	2
Acer platanoides L.	1.01		medium	4	5	11	2	2
Acer pseudoplatanus L.	1.05		medium	5	5	10	2	2
Alnus incana (L.) Moench	1.12		medium	2	4	12	2	3
Carpinus betulus L.	1.23		medium	4	5	10	11	2
Fraxinus excelsior L.	1.58		medium	4	5	11	2	2
Larix decidua Mill.	1.00		medium	3	6	11	3	2
Pinus cembra L.	1.21	*	medium	6	7	3	5	3
Tilia cordata Mill.	1.33		medium	6	7	10	3	2
Alnus glutinosa (L.) P. Gaertn.	2.77		high	3	4	10	5	2
Castanea sativa Mill.	16.84		high	6	6	9	11	2
Cornus mas L.	16.22	*	high	3	4	9	11	2
Corylus avellana L.	14.13		high	2	4	9	11	2
Crataegus laevigata (Poir.) DC. s.l.	13.11	*	high	5	5	10	2	2
Crataegus monogyna Jacq. s.l.	13.11	*	high	5	6	10	2	2
Fagus sylvatica L.	15.40		high	4	5	10	10	2
Frangula alnus Mill.	14.18	*	high	5	6	9	11	4
Juglans regia L.	26.29		high	5	5	9	10	2
Prunus padus L.	14.00	*	high	4	5	3	5	4
Prunus serotina Ehrh.	14.00	*	high	5	7	9	10	3
Pyrus communis agg.	76.09	*	high	4	5	10	11	3
Quercus cerris L.	31.77	*	high	4	4	10	10	2
Quercus petraea Liebl.	31.77	*	high	5	5	9	11	2

Species name	V_{term} **[m/s]**		V_{term} **group**	**F.B.**	**F.E.**	**S.B.**	**S.E.**	**Data source for phenology**
Quercus robur L.	31.77	*	high	5	5	9	11	2
Robinia pseudoacacia L.	12.98		high	5	6	9	4	3
Sorbus torminalis (L.) Crantz	11.13	*	high	5	6	10	1	2

Cited literature on phenology of species flowering and seed release:

1 = Müller-Schneider, P. (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. Geobotanisches Institut der ETH, Stiftung Rübel.
2 = Schütt, P., Weisgerber, H., Schuck, H.J., Lang, U.M., Roloff, A. & Stimm, B. (1995) Enzyklopädie der Holzgewächse, Handbuch und Atlas der Dendrologie [Encyclopedia of woody plants. Handbook of Dendrology]. Loose-leaf collection, illustr. ecomed Verlagsgesellschaft, Landsberg am Lech. ISBN 3-609-72030-1., 49.

3 = Hepp, C. & C., G. (2012) Baumkunde.de Online-Datenbank für Bäume und Sträucher, Rüsselsheim & Weiterstadt, Germany. http://www.baumkunde.de.

4 = Willdenow, C.L. (1820) Abbildung der deutschen Holzarten für Forstmänner und Liebhaber der Botanik. Schüppelsche Buchhandlung.

Table ii-A 2. Parameters of the turbulence measurements of each study site. Anemometer height was standardised by subtracting the mean vegetation height from the anemometer height for each site. Roughness length was set to 0.1 and frequency of turbulence measurements was 20 Hz for all sites. *ALT* = altitude (meters above sea level), *VegH* = mean vegetation height for the respective site, *HAV* = height of the anemometer above the vegetation canopy.

VegType	**Habitat**	**Site**	**Latitude**	**Longitude**	***ALT*** **[m]**	***VegH*** **[m]**	***HAV*** **[m]**	**Anemometer**
Open	Arable land	1	47°38'15"N	7°35'48"E	270	0.1	1.9	Sonic - CSAT3
Open	Grassland	2	50°56'58"N	13°30'45"E	385	0.1	2.9	Metek - USA1
Forested	Spruce forest	3	50°47'01"N	13°43'10"E	735	2.0	10.0	Metek - USA1
Forested	Spruce forest	4	50°57'49"N	13°34'01"E	380	2.7	15.0	SOLENT-R2

Table ii-A 3. Summary table for a comparison of the monthly minimum, median, mean and maximum potential migration rates. For each V_{term} and for each vegetation type, the mean values of the minimum, median, mean, and the maximum are provided.

		V_{term} (m s^{-1})		
Vegetation type	**Monthly value**	**0.4**	**1.6**	**3.2**
Open	Minimum	7.3	0.7	0.4
Open	Median	26.5	1.2	0.5
Open	Mean	115.6	1.8	0.6
Open	Maximum	930.0	9.1	2.1
Forested	Minimum	675.0	17.8	0.7
Forested	Median	2059.4	68.1	1.7
Forested	Mean	2190.7	105.3	6.5
Forested	Maximum	4457.6	444.7	33.7

Table ii-A 4. Summary statistics of the generalized linear model for the relationship between mean horizontal wind speed (*WIND*) and mean proportion of seconds that showed wind speeds greater than 4 m s^{-1} (*WIND'*). The model was based on weekly averages of both variables. The table includes estimates, standard errors (Std. Error), *t*- and corresponding *p* values for all significant interactions and variables. Different symbols indicate significant differences from gamma distribution with ***$p < 0.001$.

Vegetation type	**Estimate**	**Std. Error**	***t* value**	***p* value**	
Forested	−2.799	0.207	−13.550	<0.001	***
Open	−4.026	0.184	−21.899	<0.001	***

Table ii-A 5. Summary statistics of the generalized linear model for the effect of V_{term} species groups for each vegetation type and the proportion of species releasing their seeds on potential migration rates. The model was based on the monthly data on potential migration rates and the proportion of species releasing their seeds for both vegetation types and three different V_{term} groups provided in Figure ii-2. The table includes estimates, standard errors (Std. Error), *t*- and corresponding *p* values for all significant interactions and variables. We tested the estimates using the re-levelling procedure described by Crawley (2007). As we used a GLM with gamma error distribution family, the model coefficients (e.g. estimate) can only be interpreted if they are transformed into their reciprocal. Different symbols indicate significant differences from gamma distribution with $^{**}p < 0.01$ and $^{***}p < 0.001$.

Variable	**Estimate**	**Std. Error**	***t* value**	***p* value**	
(Intercept)	0.023	0.0037	6.290	< 0.001	***
Veg.type_Open	0.82	0.10	8.101	< 0.001	***
Vterm_Low	-0.023	0.0037	-6.160	< 0.001	***
Vterm_High	0.57	0.10	5.726	< 0.001	***
Prop.S.Release	-0.001	0.00022	-3.263	0.002	**
Veg.type_Open:Vterm_Low	-0.78	0.10	-7.722	< 0.001	***
Veg.type_Open:Vterm_High	0.45	0.26	1.770	0.0816	.
Prop.S.Release:Veg.type_Open	-0.00016	0.00061	-0.267	0.790	
Prop.S.Release:Vterm_Low	0.00072	0.00022	3.268	0.002	**
Prop.S.Release:Vterm_High	0.00	0.01	-0.109	0.913	

8.3 Project iii: Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed

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Erklärung zu den Autorenanteilen

an der Publikation: Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed.

Status (submitted, under review, in revision, accepted): accepted

Beteiligte Autoren:

- Felix Heydel (corresponding author) (FH, Promovierender)
- Sarah Cunze (SC)
- Markus Bernhardt Römermann (MBR)
- Oliver Tackenberg (OT, Betreuer)

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?

(1) zu Entwicklung und Planung

Promovierender: 55%

Co-Autor OT: 45%

(2) zur Durchführung der einzelnen Untersuchungen und Experimente

Promovierender: 80% FH führte die Computersimulationen selbstständig durch

Co-Autor OT: 20% OT parametrisierte das Simulationsprogramm PAPPUS

(3) zur Erstellung der Datensammlung und Abbildungen

Promovierender: 60% FH führte die Datenaggregierung, -aufbereitung und die Qualitätskontrolle durch. FH erstellte die Datengrundlage und Abbildungen für das oben genannte Manuskript.

Co-Autorin SC: 10% beriet bei der Berechnung der Migrationsraten

Co-Autor OT: 30% OT betreute die Abläufe der Datenarbeiten.

(4) zur Analyse und Interpretation der Daten

Promovierender: 60% FH führte die Analysen durch.

Co-Autor MBR: 20% betreute die Durchführung der statistischen Analysen

Co-Autor OT: 20% OT betreute die Durchführung der statistischen Analysen.

(5) zum Verfassendes Manuskripts

Promovierender: 70%

Co-Autorin SC: 5%

Co-Autor MBR: 5%

Co-Autor OT: 20%

8.3.1 Abstract

Long-distance dispersal (LDD) of plant seeds by wind is affected by functional traits of the species, specifically seed terminal velocity and height of seed release above the vegetation cover (HAC), as well as by the meteorological parameters wind speed and vertical turbulence. The relative importance of these parameters is still under debate and the importance of their variability in vegetation types, sites and years has only rarely been quantified. To address these topics, we performed simulation studies for different vegetation types, sites, years and plant species with PAPPUS, a process based trajectory model.

We found that LDD (measured in terms of migration rates) was higher in forests compared to open landscapes. Forests also showed greater between-year variability in LDD. Terminal velocity had an effect on LDD in both vegetation types, while the effect of HAC was significant only in the open landscape. We found considerable differences in how vertical turbulence and wind speed affect LDD between species and vegetation types: In the open landscape the strength of the positive relationship between vertical turbulence and LDD generally decreases with terminal velocity, whereas it increases in forests. The strength of the predominantly positive effect of wind speed on LDD increases with terminal velocity in both vegetation types, while in forests we found even negative relationships for species with low terminal velocity.

Our results generally suggest that the effects of vertical turbulence and wind speed on LDD by wind diverge for species with different functional traits as well as in different vegetation types.

8.3.2 Introduction

Seed dispersal and plant migration strongly affect plant diversity (Pitelka et al. 1997; Parmesan and Yohe 2003; Normand et al. 2011). The rate of future climate change is that high, that the spread rates of most plant species seem to be much lower than is required in order to keep pace with the climate induced range shifts (Neilson et al. 2005). Primarily, seed dispersal affects plant spread in space and time (Clark et al. 1998; Cain et al. 2000; Higgins et al. 2003). Long-distance dispersal (LDD) of seeds is often driven by extreme events, like rare meteorological weather conditions, large migratory animals or transport by humans (Nathan et al. 2008). LDD of seeds shapes many important and fundamental processes in plant ecology and evolution. Altogether gene flow between populations, local adaptation, spatial dynamics of plant species, communities and ecosystems are affected by LDD (e.g. Kawecki and Ebert 2004; Nathan et al. 2008; Öster et al. 2009; Latzel et al. 2011).

Regarding LDD by wind, weather conditions like convective updrafts or storms seem to play an important role. Currently the role of meteorological conditions promoting LDD is under debate: convective updrafts (Tackenberg et al. 2003b) and horizontal wind speed (Jongejans and Schippers 1999; Nathan et al. 1999; Nathan et al. 2002) were both proposed to play an important role. Unfortunately, previous studies focus on one or few species only, address either open landscapes or forests, refer to different time periods and use different simulation models. Consequently it remains unclear whether the observed and partly opposing results originate from differences between studied vegetation types, plant species, meteorological conditions or the used simulation models.

To gain general insights when addressing LDD by wind, it seems important to consider a broad range of different meteorological conditions, because of the rarity and stochasticity of conditions promoting LDD (Nathan 2006). As LDD data are difficult to acquire, the effect of the variability between vegetation types, sites and years on LDD by wind was yet only analysed in few studies. As one of the first, Houle (1998) studied temporal variation in spatial patterns of dispersed seeds empirically and found significant variation between years. Nathan et al. (2000) additionally addressed the effect of distance on LDD and found highest variation in dispersal patterns far away from the seed source.

The meteorological conditions that affect LDD by wind are not only related to the macroclimate but also depend on the structure of the vegetation type, topography and landscape texture. For example, LDD is thought to increase with landscape openness (Nathan et al. 2008). Attempts to quantify differences in LDD between vegetation types have rarely been made (e.g. Fort and Richards 1998; Tackenberg and Stöcklin 2008).

The timing of seed abscission is a further plant-controlled trait having a great impact on LDD by wind (Greene 2005; Schippers and Jongejans 2005; Greene and Quesada 2011). Seeds of many plant species are only released when the wind speed exceeds a certain release wind speed threshold, which actually leads to larger dispersal distances.

Empirical studies often use seed traps and thus regularly fail to quantify LDD (Greene and Calogeropoulos 2002). Process based trajectory models have the potential to overcome this limitation (Nathan et al. 2011). Especially for LDD by wind, process based models provide good estimates of how far seeds are expected to disperse (Nathan et al. 2002; Tackenberg

2003; Soons et al. 2004; Horn et al. 2012) and therefore supply the most accurate results of plant spread (Kuparinen 2006). In these models, seed terminal velocity during the fall (VTERM) and the height of seed release above the vegetation cover (HAC) are often considered as vital plant traits for LDD by wind (Nathan et al. 2002; Tackenberg 2003). Although the dispersed unit may also be a fruit or another morphological unit, we will use the term ‘seed’ in this study for reasons of simplification. Dispersal within the canopy seems less important and is therefore often ignored when focusing on LDD (Nathan et al. 2002). Accordingly, plant individuals dispersing their seeds above the vegetation canopy are regarded as "hot spots" of LDD by wind (Horn et al. 2001; Bohrer et al. 2008).

In this study we use a simulation approach in order to disentangle the effects of the plant traits VTERM and HAC, the meteorological parameters vertical turbulence and wind speed, between-year variability, and structure of the vegetation type (open landscape vs. forest) on LDD by wind. Specifically, we explore the following questions: (i) Does LDD differ between vegetation types? (ii) Does the effect of VTERM and HAC on LDD differ between vegetation types? (iii) Does LDD differ between years? (iv) How do the effects of vertical turbulence, wind speed, vegetation type, VTERM and HAC interact?

8.3.3 Methods

8.3.3.1 Modelling wind dispersal using PAPPUS

We used PAPPUS, a mechanistic wind dispersal model which simulates trajectories of individual seeds (for a detailed description see Tackenberg 2003). Trajectory models simulate particle trajectories so that temporary airflows (like e.g. vertical turbulence) directly affect the dispersing particle during its flight. Trajectory models provide an important increase in realism and are preferable for modelling wind dispersal over short and long distances (Kuparinen 2006). PAPPUS was validated (following Rykiel 1996) by comparing dispersal distance spectra generated by simulations with empirically observed distance spectra from release experiments in different landscapes and under various weather conditions (Tackenberg 2003). The empirically observed spectra matched reasonably well with the modelled dispersal distance spectra, especially under weather conditions with convective turbulence.

As most trajectory models, PAPPUS uses two species-specific traits to characterize plant species, namely HAC and VTERM. In the simulations, the flight of a seed is subdivided into time periods of 0.1 s, and its movement is calculated separately for each period as the sum of

VTERM and the wind vector (horizontal wind speed = WIND, direction and vertical wind speed). The decrease of wind speed with declining height above ground is taken into account by a logarithmic vertical wind profile, which is regulated by the roughness of the vegetation cover (e.g. McCartney 1990). The simulation stops once the seed falls below the closed vegetation canopy. In consequence, LDD occurs only while seeds are above the vegetation canopy (as also argued by Nathan et al. 2002).

The course of the wind vector during the flight of a seed is permanently changing due to vertical and horizontal turbulence (Mazzoni 1996). PAPPUS incorporates turbulence by deriving the course of the wind vector from high-frequency measurements of the wind vector during the period the simulations refer to. This empirical component allows realistic consideration of convective updrafts, which have been proved to be an important determinant of LDD by wind in empirical studies (Tackenberg 2003) as well as in simulation studies (Tackenberg et al. 2003b).

The simulations performed with PAPPUS result in single dispersal events which constitute discrete frequencies of dispersal distances (i.e. the dispersal kernel) when repeating simulations.

8.3.3.2 Species traits

The effect of VTERM and HAC on LDD was studied on 18 model species that were characterised by unique combinations of both traits. These trait combinations cover a wide range of relevant values, specifically VTERM of 0.1, 0.2, 0.4, 0.8, 1.6 & 3.2 m s^{-1} and HAC of 0.1, 0.4 & 1.6 m, so that results can easily be transferred to a wide range of ‘real’ plant species (see discussion for respective examples). In order to ensure direct comparability between open landscape and forest, VTERM and HAC were defined using the same values for both vegetation types. Using HAC instead of the height of seed release above ground implies that seeds of species with identical traits have identical falling heights (as the simulation only addresses dispersal above the canopy). A HAC of 0.4 m stands for example for a herb from open landscapes overtopping low vegetation cover with 0.4 m as well as for a tree overtopping the forest canopy with that height. In consequence, the results for different vegetation types are directly comparable, as the simulations refer to homogeneous landscapes, which are completely covered by the respective vegetation type.

8.3.3.3 Simulation of dispersal kernels in different environments

The most important meteorological parameter affecting seed dispersal is the course of the wind vector (wind direction, vertical and horizontal wind speed) and its fluctuations, i.e. turbulence. PAPPUS uses high-frequency measurements of the wind vector with ultrasonic anemometers to simulate the course of the wind vector. The measurements of the wind vector incorporated in our simulations address two vegetation types (open landscape and spruce forest). The measurements originate from the years 2005 and 2006 and were taken by Grünwald and Bernhofer (2007), Lehner (2008) and Prescher et al. (2010). All measured data were processed to a temporal resolution of 10 Hz. In each vegetation type, measurements were performed on two different sites (open landscape: site 1, 2 and forest: site 3, 4). For each site, the original wind data was standardised to an equal height above the vegetation cover using the logarithmic wind-profile (see also Tackenberg 2003). Further parameters of the turbulence measurements are provided in Table iii-A 1 on page 180.

For each species, vegetation type, and site we calculated 200 trajectories for each hour of the day with randomly chosen starting times within the hour. Subsequently, we aggregated these data into weekly dispersal kernels that build the basis for the further analyses. Each weekly kernel consists of 30,000 trajectories which were randomly chosen from all trajectories that were available for the respective week. The simulations refer to landscapes that are flat and completely covered by the respective vegetation type.

Two meteorological parameters were calculated for each hour and week in order to reveal the relationship between wind speed, vertical turbulence, and LDD by wind. First, we calculated WIND as the mean horizontal wind speed in 0.4 m height above the canopy. Second, we calculated TURB in that height as the proportion of LDD relevant updrafts. TURB is a measure of the intensity of vertical turbulence and is calculated as the proportion of time, during which updrafts of a vertical wind speed that is greater than the VTERM of the respective species occur (Tackenberg 2003). The time-period for which the vertical wind speed is averaged is 100 m divided by the mean horizontal wind speed. Hence, updrafts of that strength and duration are capable of prolonging the flight of a seed to reach a distance of 100 m without losing altitude in relation to the initial release height. TURB has already been used to assess the relevance of updrafts (Tackenberg et al. 2003b).

8.3.3.4 Migration rates as a measure of LDD

In order to generate a measure of LDD, we calculated migration rates following the approach presented by Clark et al. (2001). Unlike many other commonly applied measures of LDD, the calculated migration rates do not refer to a pre-determined dispersal distance (see also the discussion section). In fact, the migration rates are highly sensitive to the rare long-distance dispersal events of the species (i.e. the tail of the species' dispersal kernel). Migration rates (in m yr^{-1}) were calculated from the weekly dispersal kernels as the expected value of the maximum of a random sample of the size of the number of offspring at seed release (R_0), divided by the generation time (T, see also Higgins et al. 2003). R_0 was set 100 and T to 1.

8.3.3.5 Data analysis

To test whether the calculated migration rates can generally be used as a measure of LDD, we tested the strength of relationship between migration rates and an alternative measure of LDD. Therefore, we exemplarily calculated the Spearman correlation coefficient ρ between the proportion of seeds exceeding 100 m reference distance (further referred to as 'alternative measure of LDD') and the calculated migration rates. In order to simplify our argument, we will mostly refer to LDD rather than to migration rates in the following.

The availability of wind data varied between vegetation types, sites, and years (for weekly values of TURB and WIND of the four sites and both years see Table iii-A 2 on page 181). Thus, we generated customized datasets based on the same periods. These subsets were compiled in respect of sample size and comprised weeks from the whole year. This subsetting ensures that the comparison between vegetation types is not biased by the consideration of different periods of the year with different weather conditions.

The effect of vegetation types, sites, VTERM and HAC on LDD was analysed using 17 identical weeks from the year 2006 (dataset 1, see Table iii-A 2). The analysis of the between-year effect on LDD was based on 12 and 19 identical weeks from both years 2005 and 2006 (dataset 2 and 3 for open landscape sites and forest sites, respectively). The analyses of the relationship between the calculated migration rates and the alternative measure of LDD, as well as the effect of WIND and TURB on LDD, were both based on 49 and 51 weeks from 2005 and 2006 (dataset 4 and 5 for open landscape sites and forest sites, respectively).

Statistical analyses were done using generalised linear models (GLM) of the gamma error distribution family.

First, we analysed the effect of vegetation type with a GLM containing the variables vegetation type (explanatory variable) and LDD (dependent variable). Subsequently, we studied the effects of sites, VTERM and HAC on LDD with separate GLMs for each vegetation type. To analyse the between-year effect on LDD, four separate GLMs (one model for each site) were set up containing VTERM and year as explanatory variables. In order to analyse the between-year effect on LDD for each species separately, here VTERM was treated as a factor.

Models were simplified using backward selection of the non-significant variables until the final minimal adequate model contained only significant terms ($p < 0.05$) and a minimal Akaike Information Criterion (AIC) was obtained (Crawley 2007).

To analyse the effect of WIND and TURB on LDD and to detect differences between species and vegetation types, we calculated Spearman correlation coefficients ρ between these parameters and LDD separately for each VTERM (HAC = 0.4 m) and vegetation type.

All statistical analyses were performed with R 2.14.1 (R Core Team 2012).

8.3.4 Results

8.3.4.1 Migration rates as a measure of LDD

The analysis of the relationship between calculated migration rates and the alternative measure of LDD showed that both are highly correlated (Spearman's $\rho = 0.965$; $p < 0.001$).

8.3.4.2 Vegetation types and sites

We found significantly higher LDD in forest sites than in open landscape sites ($p < 0.001$, Table iii-1 and Figure iii-1). In forest sites, mean TURB was about 24 times higher and mean WIND about 30 % higher than in open landscape sites (Table iii-2). The effect of site on LDD was significant in both vegetation types. Between forest sites absolute differences in median migration rates were bigger than between open landscape sites (Figure iii-1), whereby relative differences in LDD between sites were greater in open landscape sites than in forest sites. In open landscape sites, we found 60 % greater median migration rates in site 1 than in site 2 while in forest sites we found 38 % greater median migration rates in site 4 than in site 3. Similarly, relative between-site differences in TURB and WIND (Table iii-2) were greater between the open landscape sites (site 1 showed about four times higher TURB and 22 % higher WIND than site 2) than between the forests sites (site 3 showed about 55 % smaller TURB and 13 % higher WIND than site 4).

Table iii-1: Summary statistics of three generalised linear models (GLM) of the gamma error distribution family. The first model analyses the effect of vegetation types on migration rates. The second and third model analyse the effect of site, seed terminal velocity (VTERM) and height of seed release above the vegetation cover (HAC) on migration rates separately for open landscape and forest. Each model bases on 1224 migration rates (17 weeks × 18 species × 4 sites × 1 year). It must be taken into account, that the model coefficients of a GLM using the gamma error distribution family can only be interpreted if the coefficient (e.g. estimate) is transformed into its reciprocal. The table includes estimates, standard errors (Std. Error), t- and corresponding p-values for all significant interactions and variables. Different symbols indicate significant levels with ***p < 0.001, *p < 0.05.

	Estimate	**Std. Error**	**t-value**	**p-value**	
1) Vegetation type					
Open landscape	0.00226	0.00023	9.820	< 0.001	***
Forest	–0.00155	0.00022	–6.452	< 0.001	***
2) Open landscape					
Site1	–0.00890	0.00156	–5.701	< 0.001	***
Site2	0.00225	0.00092	2.438	0.015	*
VTERM	0.09241	0.01546	5.978	< 0.001	***
HAC	0.00411	0.00107	3.850	< 0.001	***
VTERM:HAC	–0.04230	0.01055	–4.012	< 0.001	***
3) Forest					
Site3	0.00006	0.00005	1.997	0.231	
Site4	–0.00015	0.00004	–4.102	< 0.001	***
VTERM	0.00316	0.00020	15.683	< 0.001	***
HAC	0.00006	0.00003	1.917	0.056	
VTERM:HAC	–0.00080	0.00017	–4.709	< 0.001	***

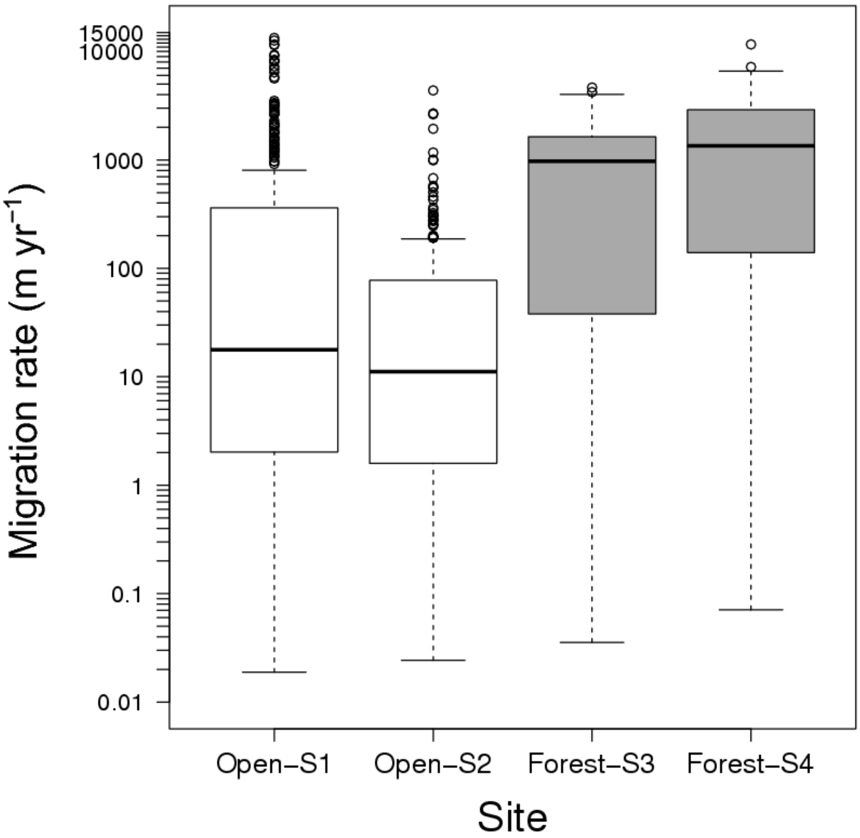

Figure iii-1: Migration rates for four sites of the vegetation types open landscape (S1, S2) and forest (S3, S4). Each box plot represents 306 migration rates (17 weeks × 18 species). Migration rate is shown on a log-scaled axis.

8.3.4.3 Species traits: VTERM and HAC

VTERM had an effect on LDD in both vegetation types (Table iii-1). A significant effect of HAC on LDD was found only in open landscape sites ($p < 0.001$) while the interaction of VTERM and HAC was significant in both vegetation types. Low median migration rates (of only few m yr^{-1}) were found for open landscape species with VTERM ≥ 1.6 m s^{-1} and for forest species with VTERM = 3.2 m s^{-1} (Figure iii-2).

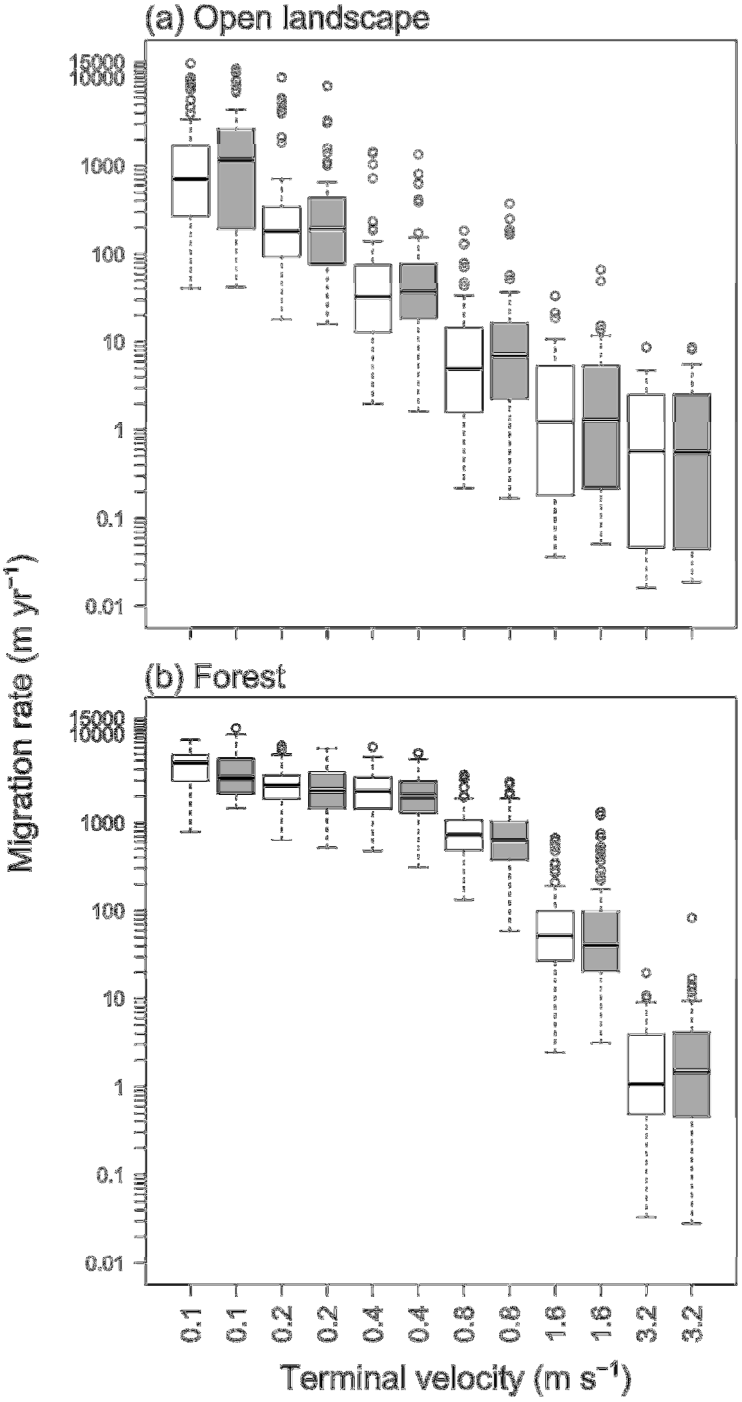

Figure iii-2: Migration rates for the years 2005 (white) and 2006 (grey) in the vegetation type open landscape (a) and forest (b). Each box plot represents 432 (open landscapes) or 684 (forests) migration rates: 18 species × 2 sites × 12 (19) weeks. Migration rate is shown on a log-scaled axis.

8.3.4.4 Between-year variability and interaction with VTERM

A significant between-year effect on LDD was only found in forest sites (Table iii-3and Figure iii-2b). Absolute between-year differences in LDD increased with decreasing VTERM and were biggest for species with VTERM = 0.1 m s^{-1} and smallest for species with

VTERM = 3.2 m s^{-1} (difference in median migration rates: 1501.8 and 0.4 m yr^{-1}, respectively). The between-year effect on LDD was different between both forest sites: In forest site 3 the between-year effect on LDD was generally significant (Table iii-3). By contrast, in the forest site 4 the between-year effect on LDD was only significant for species with intermediate and high VTERM (1.6 and 3.2 m s^{-1}) although for these species absolute differences in median migration rates were only about a few decimetres per year.

Relative between-year differences in TURB were greater in forest site 3 (21.6%) than in site 4 (0.6 %), whereas between-year differences in WIND were greater in site 4 (4.6%) than in site 3 (0.5%; see also Table iii-2).

In open landscape sites, absolute between-year differences in LDD were only high for species with VTERM = 0.1 m s^{-1} (difference in median migration rates: 457.1 m yr^{-1}, see also Figure iii-2a).

Table iii-2: Summary table of the meteorological parameters TURB (the proportion of updrafts relevant for long-distance seed dispersal as described in Tackenberg et al. 2003b) and WIND (horizontal wind speed). Mean values and standard deviation (SD) were calculated based on the weekly values of TURB and WIND (in m s–1) provided in Table iii-A 2 (supplementary material). The column "Factor" labels the factor considered for quantifying differences in TURB and WIND. Open = open landscape, veg. = vegetation.

					Meteorological parameter			
					TURB		WIND	
Dataset	**Factor**	**Veg. type**	**Site**	**Year**	**Mean**	**SD**	**Mean**	**SD**
1	Veg. type	Open	1, 2	2006	0.01	0.01	1.18	0.33
1	Veg. type	Forest	3, 4	2006	0.17	0.09	1.53	0.22
1	Site	Open	1	2006	0.01	0.01	1.07	0.33
1	Site	Open	2	2006	< 0.01	< 0.01	1.29	0.30
1	Site	Forest	3	2006	0.12	0.11	1.62	0.20
1	Site	Forest	4	2006	0.21	0.05	1.44	0.20
2	Year	Open	1	2005	0.01	0.01	1.07	0.42
2	Year	Open	1	2006	0.01	0.01	1.12	0.36
2	Year	Open	2	2005	0.01	< 0.01	1.31	0.53
2	Year	Open	2	2006	< 0.01	< 0.01	1.31	0.28
3	Year	Forest	3	2005	0.15	0.10	1.60	0.30
3	Year	Forest	3	2006	0.12	0.09	1.61	0.30
3	Year	Forest	4	2005	0.20	0.04	1.37	0.21
3	Year	Forest	4	2006	0.20	0.04	1.43	0.25

8.3.4.5 The effect of the meteorological parameters WIND and TURB

The effect of WIND and TURB on LDD differed between vegetation types (Table iii-4, Figure iii-3). In forest sites, TURB was positively correlated to LDD for species with VTERM $\geq$ 0.8 m s^{-1} and the effect of WIND on LDD changed from positive (VTERM = 3.2 m s^{-1}) to negative (VTERM $\leq$ 0.4 m s^{-1}).

In open landscape sites, LDD was positively related to TURB for species with VTERM $\leq$ 1.6 m s^{-1} and WIND was positively correlated to LDD for species with VTERM $\geq$ 0.8 m s^{-1}.

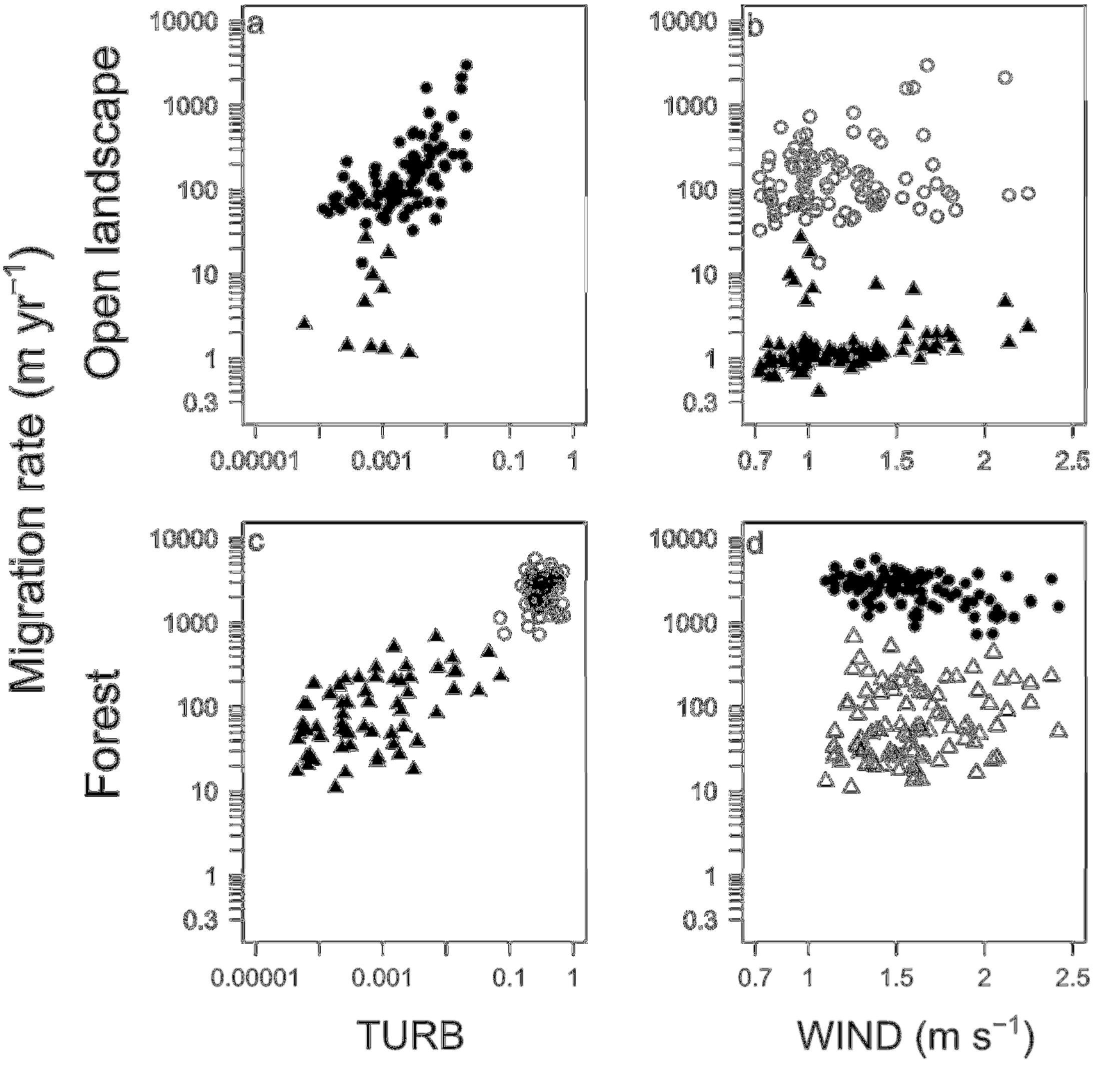

Figure iii-3: Relationship between migration rates and both studied meteorological parameters TURB (the proportion of updrafts relevant for long-distance seed dispersal as described in Tackenberg et al. 2003b) and WIND (horizontal wind speed). The relationship is shown for selected species from the open landscape and forest with seed terminal velocity = 0.2 m s–1 (circles) and 1.6 m s–1 (triangles). Full symbols indicate significant correlations between migration rates and the respective meteorological measure (Table iii-4). The plots show 182 and 198 migration rates and corresponding meteorological parameters for open landscape and forest, respectively. Migration rate and TURB are shown on a log-scaled axis.

Table iii-3: Summary statistics of four generalised linear models of the gamma error distribution family. Each model analyses the between-year effect on migration rates for one site of the vegetation types open landscape and forest. Models are based on 432 and 684 migration rates: 18 species × 1 site × 2 years × 12 and 19 weeks for analysis of open landscape and forest, respectively. The table includes estimates, standard errors (Std. Error), t- and corresponding p-values for all significant interactions and variables. Between-year differences were only significant when the variable 'year' or its interaction with seed terminal velocity (VTERM) showed a significant effect on migration rates. Different symbols indicate significant levels with ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

	Estimate	**Std. Error**	**t-value**	**p-value**
Open landscape: Site 1				
VTERM_0.1	0.00027	0.000056	4.837	< 0.001***
VTERM_0.2	0.00058	0.00018	3.137	0.002**
VTERM_0.4	0.0055	0.0012	4.606	< 0.001***
VTERM_0.8	0.029	0.0061	4.793	< 0.001***
VTERM_1.6	0.198	0.041	4.831	< 0.001***
VTERM_3.2	0.802	0.16	4.836	< 0.001***
Open landscape: Site 2				
VTERM_0.1	0.0019	0.00029	6.832	< 0.001***
VTERM_0.2	0.0048	0.0010	4.644	< 0.001***
VTERM_0.4	0.025	0.004	6.317	< 0.001***
VTERM_0.8	0.136	0.020	6.733	< 0.001***
VTERM_1.6	0.457	0.067	6.802	< 0.001***
VTERM_3.2	1.146	0.168	6.820	< 0.001***
Forest: Site 3				
VTERM_0.1	0.00028	0.000039	7.316	< 0.001***
VTERM_0.2	0.00019	0.000066	2.951	0.003**
VTERM_0.4	0.00018	0.000065	2.837	0.005**
VTERM_0.8	0.00078	0.00012	6.329	< 0.001***
VTERM_1.6	0.0082	0.00090	9.083	< 0.001***
VTERM_3.2	0.495	0.052	9.467	< 0.001***
Year	0.00012	0.000053	2.250	0.025*
Forest: Site 4				
VTERM_0.1	0.00018	0.000024	7.566	< 0.001***
VTERM_0.2	0.00010	0.000045	2.289	0.022*
VTERM_0.4	0.00017	0.000052	3.234	0.001**
VTERM_0.8	0.0011	0.00017	6.436	< 0.001***
VTERM_1.6	0.014	0.0019	7.468	< 0.001***
VTERM_3.2	0.525	0.069	7.563	< 0.001***
Year	0.0000034	0.000034	0.098	0.922
VTERM_0.2:Year	−0.0000044	0.000063	−0.070	0.944
VTERM_0.4:Year	0.000014	0.000075	0.185	0.853
VTERM_0.8:Year	−0.000017	0.00024	−0.071	0.943
VTERM_1.6:Year	−0.0054	0.0022	−2.478	0.013*
VTERM_3.2:Year	−0.287	0.076	−3.768	< 0.001***

8.3.5 Discussion

Plant spread is mainly driven by rare LDD events (Cain et al. 2000; Nathan 2006). Many studies addressing LDD define it either via absolute dispersal distances (for dispersal of aquatic invertebrates by birds e.g. Green and Figuerola 2005), a percentile of dispersal distances (e.g. the 99th percentile of dispersal distances, Soons and Ozinga 2005) or the proportion of dispersal events exceeding a pre-determined reference distance (e.g. Tackenberg 2003). To generate a measure of LDD, we calculated migration rates which are highly sensitive to rare long-distance dispersal events. For instance, migration rates of species with high VTERM may be much lower than migration rates of species with low VTERM. However, these low migration rates represent the longest dispersal events for these species. Hence, these low migration rates are likely to be ecologically relevant, even if they are lower than pre-determined dispersal distances (as commonly used for other measures of LDD). In addition, we exemplarily showed that the migration rates are closely related to an alternative measure of LDD that refers to a pre-determined dispersal distance of 100 m. Thus, we assume that migration rates can be used as a general measure of LDD and refer to the term LDD rather than to migration rates in order to keep the discussion general and simple. However, for addressing specific questions, concerning e.g. LDD in heavily fragmented landscapes, measures of LDD which for example refer to a particular dispersal distance may be more suitable.

8.3.5.1 Meteorological conditions: the effect of TURB and WIND

Wind can be a very effective dispersal vector, but only if the duration of the flight of a seed is prolonged by turbulence or updrafts above the vegetation cover (Nathan et al. 2002). Above the vegetation cover, open landscapes and forests generally differ with respect to the surface roughness. Over any surface, the surface drag generates vertical gradients in horizontal wind velocity and sheer-driven eddies. Above the forest canopy, where surface roughness often is higher, the surface drag is stronger and generates more shear-driven turbulence than e.g. above the vegetation cover of open landscapes (Stull 1988; Finnigan and Kaimal 1994). Everywhere where the sun is providing energy to the surface, thermally driven buoyant eddies are generated by heat fluxes with warmer and lighter air near the surface (Stull 1988; Finnigan and Kaimal 1994). Heat fluxes may be weaker above forests than above open landscapes, as more of the solar energy is likely to be converted into fluxes of water vapour. Thus, above open landscapes surface characteristics enhancing the generation of vertical turbulence can be suggested to be more often found than above forest canopies (Stull 1988). Thermally driven updrafts generally tend to generate eddies that provide lift for longer and continuous periods than shear driven turbulence produced by strong winds. In summary, open landscapes and forests differ with respect to the relative distribution of turbulence and its resident time above the vegetation cover. Above most open landscapes, we suggest that more thermally driven buoyant eddies, providing lift for longer periods, are generated. By contrast, above forest canopies we suggest high wind speeds tend to produce strong, but more intermittent, shear driven turbulence (Finnigan and Kaimal 1994).

We found both TURB and WIND to be related to LDD in both vegetation types. In both vegetation types the strength of the predominantly positive relationship between WIND and LDD generally increased with VTERM. Interestingly, even WIND showed a negative effect on LDD of tree species with VTERM ≤ 0.4 m s^{-1}. This negative effect of WIND on LDD of tree species with low VTERM could possibly be explained by the tendency of shear-driven turbulence above the canopy becoming more intermittent when wind velocity is increasing. Although shear-driven turbulence generated by strong winds can be strong, its intermittency probably makes it less effective for LDD by wind. Furthermore, species interactions with TURB differed considerably between vegetation types. In forest sites, the strength of the positive relationship between TURB and LDD generally increased with VTERM and was significant for species VTERM ≥ 0.8 m s^{-1}. For tree species with morphological adaptations to dispersal by wind (e.g. species with winged seeds like *Pinus nigra* (VTERM = 0.81 m s^{-1}) and *Fraxinus excelsior* (VTERM = 1.58 m s^{-1}) we suggest that TURB plays an important role for LDD. For tree species with high VTERM (e.g. *Alnus glutinosa* with VTERM = 2.77 m s^{-1}) we found both WIND and TURB to have a significant effect on LDD although it yields in only small dispersal distances and may thus not be ecologically relevant at all.

Our results from open landscape sites suggest that the strength of the positive relationship between TURB and LDD generally decreases with VTERM. Thus, we propose updrafts to play a predominant role for LDD of open landscape species with low and intermediate VTERM which is in strong accordance with previous findings made by Tackenberg et al. (2003b) and was also empirically observed (Tackenberg 2003, see also section 2.1).

For species with higher VTERM, LDD was stronger affected by WIND than by TURB in both vegetation types. This particular role of WIND could possibly explained by the tendency of shear driven turbulence being stronger (even though more intermittent) than thermally driven turbulence.

Table iii-4: Correlations between migration rates and both studied meteorological parameters TURB (the proportion of updrafts relevant for long-distance seed dispersal as described in Tackenberg et al. 2003b) and WIND (horizontal wind speed). Correlation analyses were carried out for each seed terminal velocity (VTERM) and each vegetation type and based on 546 and 594 migration rates and corresponding meteorological parameters for open landscape and forest, respectively. Different symbols indicate significance levels with ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

		Meteorological parameter					
		TURB			***WIND***		
Vegetation type	VTERM (m s^{-1})	Spearman's ρ	p-value		Spearman's ρ	p-value	
Open landscape	0.1	0.557	< 0.001	***	0.018	0.866	
Open landscape	0.2	0.641	< 0.001	***	0.075	0.477	
Open landscape	0.4	0.482	< 0.001	***	0.179	0.090	
Open landscape	0.8	0.502	< 0.001	***	0.334	0.001	**
Open landscape	1.6	0.383	< 0.001	***	0.418	< 0.001	***
Open landscape	3.2	0.121	0.252		0.497	< 0.001	***
Forest	0.1	0.136	0.178		−0.374	< 0.001	***
Forest	0.2	0.133	0.187		−0.378	< 0.001	***
Forest	0.4	0.120	0.237		−0.452	< 0.001	***
Forest	0.8	0.522	< 0.001	***	−0.079	0.433	
Forest	1.6	0.539	< 0.001	***	0.197	0.051	
Forest	3.2	0.401	< 0.001	***	0.479	< 0.001	***

8.3.5.2 Differences between vegetation types and sites

Our results show that LDD was significantly greater above the canopy of the forest sites than above the open landscape sites. Especially in fragmented landscapes, open landscapes are typically surrounded by aboveground barriers like e.g. forests, hedges or shrubs. Such aboveground barriers are supposed to decrease LDD by decreasing wind speed (Nathan et al. 2008). By contrast, forests hardly exhibit higher aboveground barriers decreasing wind speed above their canopy (Stull 1988). Hence, lower LDD above the open landscape sites may be due to aboveground barriers surrounding them. By analysing plant communities in The Netherlands, Ozinga et al. (2004) showed a clear positive relationship between increasing openness of the vegetation and the potential of species' LDD by wind.

Our results indicate that somewhat greater relative differences in LDD between open landscape sites than between forest sites may be explained by greater relative between-site differences in TURB and WIND in open landscape sites than in forest sites. However, as the analysis of the between-site effect was performed only for two sites, the obtained differences between sites cannot be referred to particular site characteristics and should not be generalized from our study.

8.3.5.3 The effect of the species traits VTERM and HAC

Our result of the significant importance of VTERM on LDD by wind is supported by early findings of Green (1980) and subsequent studies (Tackenberg et al. 2003a; Wright et al. 2008). The effect of HAC was not significant in forest sites, but in open landscape sites. Hence, tall species from open landscapes like e.g. *Typha latifolia* (VTERM = 0.11 m s^{-1}, all VTERM data mentioned in the following retrieved from Hintze et al. 2013) have a considerably higher probability to exhibit LDD by wind than low-growing species with similar VTERM as e.g. *Tussilago farfara* (VTERM = 0.17 m s^{-1}).

However, HAC must be interpreted differentially when comparing herbs and forest trees: It seems rather unrealistic that a variability of 1.5 m in HAC occurs within one small growing herb-species (much less within individuals), while such variability can easily be observed within single tree individuals. From an evolutionary point of view it would therefore be interesting to investigate, whether lowering VTERM or increasing HAC is a more successful evolutionary process of plant species in response to selection on LDD. In a simulation study regarding wind dispersal in grasslands species Soons et al. (2004) found a greater effect of release height on LDD in comparison to VTERM when considering the magnitude of observed *within*-species variability of these traits.

For open landscape species with intermediate and high VTERM as well as for forest species with high VTERM wind dispersal yielded in only very low dispersal rates. Hence, we suggest that for these species other vectors than wind play a bigger role for seed dispersal.

8.3.5.4 Between-year variability

Regarding forest sites, our results indicate that between-year differences in LDD are significant. The between-year effect was generally significant in site 3. By contrast, in site 4 only species with intermediate and high VTERM (e.g. *Fraxinus excelsior* and *Alnus glutinosa* exhibiting a VTERM of 1.58 and 2.77 m s^{-1}, respectively) showed a significant between-year effect on LDD (Table iii-3). Despite the significance of the between-year effect in site 4, its ecological relevance is very likely to be only minor as the absolute between-year differences in LDD were less than few meters only. In agreement with our findings for forest site 3, considerable between-year variability was also found in low VTERM and wind dispersed

Betula alleghaniensis and *Pinus halepensis* (Houle 1998; Nathan et al. 2000, respectively). For species with intermediate VTERM, Gomez-Aparicio et al. (2007) found no considerable between-year variability in Mediterranean *Acer opalus* (VTERM =1.04 m s^{-1}, unpublished data). In open landscape sites, the between-year differences of LDD were relatively small for most species (except for species with VTERM = 0.1 m s^{-1}, Figure iii-2a) and not significant.

Our results from forest sites suggest that site-specific characteristics seem to play an important role for between-year variability in LDD. This finding is probably due to site-specific differences in frequency and magnitude of meteorological conditions favouring uplift of seeds. Shear-induced uplifting of tree seeds is known to be influenced by the density of the canopy and vegetation cover (Bohrer et al. 2008) which is likely to differ between the forest sites analysed in this study. In fact, for the forest sites, the observed site-specific between-year differences in LDD might be explained by between-year differences in the occurrence and strength of meteorological parameters: between-year differences in TURB were greater in forest site 3, whereas between-year differences in WIND were greater in site 4. This pattern tentatively indicates, that the general between-variability in LDD for site 3 may be explained by considerable between-year variability in TURB. By contrast, the pronounced variability of LDD for species with VTERM ≥ 1.6 m s^{-1} in site 4 could be due to greater between-year differences in WIND.

Kuparinen et al. (2009) found biggest differences in LDD for species with low VTERM. Likewise, our results show that absolute between-year differences in LDD in both vegetation types were biggest for species with low VTERM. Hence, the variability at the between-year time scale is likely to affect spread rates of species with low VTERM to a greater extent than spread rates of species with high VTERM.

Although we put considerable effort in collecting wind data from different years and different sites, the merged datasets allowed conducting a reliable between-year analysis for the years 2005 and 2006, only. Consequently, the results from the between-year analysis should not be generalized.

8.3.5.5 Conclusions and outlook

To conclude, we found that LDD was higher in forests than in open landscapes. Forests also showed greater between-year variability in LDD. In both vegetation types, VTERM had an effect on LDD, while the effect of HAC was significant only in the open landscape. Our results show considerable differences in how TURB and WIND affected LDD between species and vegetation types. Until now, such differences - if recognized at all - have often been attributed to differences in model performance. However, to further elaborate the role of the considered parameters, and their variability and interaction on LDD by wind, additional studies comprising even data sets from further study sites and larger temporal scales (e.g. decades of environmental data) seem vitally important. As the availability of wind shows a considerable within-year variation, the effects of TURB and WIND on LDD are likely to differ in the course of the year. By focussing our analysis on the same periods of the year we prevented comprising biased data with respect to within-year variability of TURB and WIND. In our study, seed abscission was not addressed. Seed abscission can follow a seasonal pattern and positively affect LDD when it preferably occurs during periods of prolonged updrafts (Maurer et al. 2013). Likewise, seed abscission during high wind speed events was shown to positively affect LDD (Pazos et al. 2013) and thereby decreasing differences in LDD between low and high wind speed environments. Due to the exclusion of seed abscission, our results could partially underestimate LDD, particularly in the open landscape (as a low wind speed environment). For future studies, the effect of the phenology of dispersal on LDD should be analysed in detail promising deeper understanding of its role for species' LDD. For example, LDD of forest species dispersing in summer time (e.g. *Ulmus laevis*) vs. LDD of forest species dispersing in winter time (e.g. *Acer platanoides*) is likely to be differentially affected by meteorological parameters, even if VTERM of the species is quite similar.

8.3.6 Acknowledgements

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8.3.8 Supplementary material

Table iii-A 1: Parameters of the turbulence measurements of each study site. Anemometer height was calculated by subtracting the mean vegetation height from the anemometer height for each site. Roughness length was 0.1 and frequency of turbulence measurements was 20 Hz for all sites. VegType = vegetation type, ALT = altitude (meters above sea level), VegH = mean vegetation height for the respective site, HAV = height of the anemometer above the vegetation canopy, Open = open landscape.

VegType	**Site**	**Latitude**	**Longitude**	**ALT (m)**	**VegH (m)**	**HAV (m)**	**Anemometer**
Open	1	47°38'15"N	7°35'48"E	270	0.1	1.9	Sonic - CSAT3
Open	2	50°56'58"N	13°30'45"E	385	0.1	2.9	Metek - USA1
Forest	3	50°47'01"N	13°43'10"E	735	2.0	10.0	Metek - USA1
Forest	4	50°57'49"N	13°34'01"E	380	2.7	15.0	Solent - R2

Table iii-A 2: Mean weekly meteorological parameters, specifically TURB (T = the proportion of updrafts relevant for long-distance seed dispersal as described in Tackenberg et al. 2003b) and WIND (W = horizontal wind speed in m s-1). TURB was averaged considering all values of seed terminal velocity (VTERM). Dataset 1 labels 17 identical weeks (marked with an "x") used for analysing the effect of vegetation types, sites, VTERM and HAC (year 2006 only). Dataset 2 and 3 label 12 and 19 identical weeks used for the analysis of between-year variability (for open landscape and forests, respectively). Dataset 4 and 5 label 49 and 51 identical weeks used for analysing the effect of meteorological conditions on long-distance seed dispersal from the years 2005 and 2006 for open landscape sites and forest sites, respectively. WN = week number, NA = data not available.

						Open landscape								**Forest**							
						Site 1				**Site 2**				**Site 3**				**Site 4**			
	Dataset					**2005**		**2006**		**2005**		**2006**		**2005**		**2006**		**2005**		**2006**	
WN	1	2	3	4	5	T	W	T	W	T	W	T	W	T	W	T	W	T	W	T	W
1						NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2				x	x	NA	NA	0.00	1.75	NA	NA	0.00	0.88	NA	NA	NA	NA	0.22	2.10	0.22	1.29
3				x	x	NA	NA	0.00	1.52	NA	NA	0.01	1.80	NA	NA	NA	NA	0.25	2.13	0.28	1.96
4				x	x	NA	NA	0.01	1.09	NA	NA	0.00	0.87	NA	NA	NA	NA	0.24	1.62	0.31	2.05
5				x	x	NA	NA	0.00	0.59	NA	NA	0.00	1.04	NA	NA	0.07	1.80	0.19	1.70	0.22	1.30
6	x			x	x	NA	NA	0.01	0.86	0.01	1.44	0.00	1.92	NA	NA	0.07	2.06	0.26	1.64	0.25	1.81
7	x	x		x	x	0.02	2.14	0.00	1.34	0.01	2.09	0.00	1.43	NA	NA	0.03	1.68	0.32	2.38	0.19	1.58
8	x	x		x	x	0.00	1.03	0.01	0.95	0.01	1.04	0.02	1.29	NA	NA	0.36	1.59	0.22	1.26	0.32	1.47
9	x	x		x	x	0.01	1.40	0.02	1.68	0.00	1.42	0.00	1.63	NA	NA	0.08	1.62	0.22	1.49	0.21	1.55
10	x	x		x	x	0.02	1.34	0.01	1.58	0.00	2.07	0.00	1.61	NA	NA	0.06	1.80	0.22	1.81	0.21	1.49
11	x	x		x	x	0.04	1.18	0.00	1.23	0.01	2.17	0.00	1.14	NA	NA	0.40	1.54	0.19	2.03	0.30	1.14
12	x	x	x	x	x	0.01	1.01	0.00	1.40	0.01	0.96	0.00	1.09	0.13	1.47	0.10	1.60	0.20	1.22	0.20	1.22
13	x	x	x	x	x	0.00	1.01	0.03	1.43	0.02	0.94	0.00	1.68	0.23	1.39	0.03	1.98	0.25	1.09	0.18	1.81
14	x		x	x	x	NA	NA	0.01	1.17	0.01	1.40	0.00	1.34	0.10	1.65	0.04	1.49	0.22	1.67	0.15	1.55
15	x		x	x	x	NA	NA	0.00	1.21	0.00	0.84	0.00	1.42	0.14	1.21	0.11	1.65	0.16	1.09	0.18	1.45
16	x		x	x	x	NA	NA	0.00	0.81	0.01	1.17	0.00	1.14	0.39	1.71	0.05	1.46	0.29	1.34	0.15	1.32
17			x	x	x	NA	NA	0.01	0.94	0.00	0.91	NA	NA	0.14	1.39	0.13	1.15	0.16	1.12	0.18	1.06
18			x	x	x	NA	NA	NA	NA	0.00	1.37	NA	NA	0.06	1.62	0.26	1.75	0.15	1.41	0.28	1.45
19			x	x	x	NA	NA	NA	NA	0.00	1.55	0.00	1.00	0.11	1.78	0.36	1.66	0.19	1.45	0.24	1.31
20				x	x	NA	NA	0.02	1.14	0.00	1.11	0.00	1.42	0.12	1.40	NA	NA	0.21	1.23	0.23	1.64
21				x	x	NA	NA	NA	NA	0.00	0.92	NA	NA	0.06	1.38	NA	NA	0.16	1.28	0.23	1.82
22				x	x	NA	NA	0.00	1.05	0.00	1.21	0.00	1.73	0.09	1.64	NA	NA	0.18	1.41	NA	NA
23				x	x	NA	NA	0.00	0.94	0.00	1.53	0.00	1.16	0.10	1.98	0.14	1.48	0.21	1.62	NA	NA
24	x			x	x	NA	NA	0.00	0.65	0.00	1.42	0.00	0.83	NA	NA	0.19	1.30	0.16	1.39	0.18	1.15
25			x		x	NA	NA	NA	NA	NA	NA	NA	NA	0.15	1.62	0.09	1.31	0.20	1.31	0.16	1.24
26			x	x	x	0.00	0.69	0.00	0.61	0.00	1.03	NA	NA	0.08	1.34	0.22	1.36	0.15	1.25	0.22	1.21
27			x	x	x	0.00	0.86	NA	NA	0.00	0.97	0.01	1.31	0.11	1.36	0.26	1.78	0.17	1.20	0.28	1.43
28				x	x	0.01	0.73	NA	NA	0.00	0.87	NA	NA	NA	NA	0.18	1.18	0.20	1.18	0.19	1.13
29				x	x	0.01	0.93	NA	NA	NA	NA	0.00	0.85	NA	NA	0.21	1.29	0.16	1.23	0.18	1.16
30				x	x	0.01	0.78	NA	NA	NA	NA	0.00	0.75	0.07	1.40	NA	NA	NA	NA	0.18	1.13
31			x	x	x	0.02	0.91	NA	NA	NA	NA	0.00	1.21	0.06	1.46	0.06	1.50	0.17	1.47	0.20	1.46

32	x	x		x	x	0.01	0.76	0.02	0.75	0.00	1.44	0.00	1.22	NA	NA	0.10	1.63	0.14	1.46	0.22	1.51
33	x	x	x	x	x	0.02	0.85	0.01	0.86	0.00	0.94	0.00	1.05	0.18	1.45	0.07	1.39	0.20	1.27	0.19	1.34
34	x		x	x	x	0.02	0.95	0.02	0.84	NA	NA	0.00	1.22	0.26	1.28	0.04	1.60	0.17	1.28	0.15	1.41
35				x	x	0.01	0.66	0.01	0.76	NA	NA	0.00	1.65	NA	NA	NA	NA	0.19	1.15	0.18	1.70
36		x		x	x	0.00	0.73	0.02	0.82	0.00	0.83	0.00	1.64	NA	NA	NA	NA	0.21	1.26	0.21	1.73
37				x	x	0.01	0.74	NA	NA	0.00	1.15	0.01	1.23	NA	NA	0.24	2.28	0.16	1.25	NA	NA
38	x	x		x	x	0.01	0.73	0.01	0.73	0.00	0.82	0.01	1.12	0.30	1.62	0.16	1.78	NA	NA	0.27	1.41
39	x	x	x	x	x	0.00	0.61	0.01	0.70	0.00	0.95	0.01	0.86	0.04	1.45	0.16	1.43	0.15	1.40	0.22	1.23
40			x	x	x	0.03	0.97	0.01	0.87	0.00	1.08	NA	NA	0.30	1.76	0.03	1.66	0.26	1.37	0.18	1.62
41			x	x	x	0.00	0.72	NA	NA	0.00	1.11	0.00	0.78	0.19	2.05	0.11	1.40	0.27	1.52	0.17	1.20
42				x	x	0.00	1.05	NA	NA	0.00	0.94	0.00	0.97	0.20	1.82	0.09	1.86	NA	NA	0.21	1.36
43			x	x	x	0.00	0.80	NA	NA	0.00	1.43	0.00	1.73	0.05	1.99	0.04	1.93	0.21	1.81	0.25	1.85
44			x	x	x	0.00	1.18	NA	NA	0.00	1.46	0.00	2.25	0.03	2.41	0.09	2.48	0.22	1.73	0.25	2.04
45					x	NA	NA	NA	NA	NA	NA	NA	NA	0.03	1.67	0.07	2.73	NA	NA	NA	NA
46				x	x	NA	NA	NA	NA	0.00	1.18	0.00	1.79	0.04	1.78	0.05	2.19	NA	NA	0.21	1.87
47				x	x	NA	NA	NA	NA	0.00	1.63	0.00	1.84	0.16	1.76	0.03	1.96	0.29	1.71	NA	NA
48				x	x	NA	NA	NA	NA	0.00	0.97	0.00	0.98	0.05	1.57	0.03	1.74	0.20	1.37	NA	NA
49				x	x	NA	NA	NA	NA	0.00	1.40	0.00	2.14	0.05	1.73	0.04	2.05	0.19	1.57	NA	NA
50				x	x	NA	NA	NA	NA	0.00	1.81	0.00	1.82	0.06	2.07	0.04	2.07	0.20	1.87	NA	NA
51				x	x	0.00	1.01	NA	NA	0.00	2.26	0.00	1.04	0.07	2.45	NA	NA	0.21	1.88	NA	NA
52				x	x	NA	NA	NA	NA	0.00	1.57	0.00	1.06	0.13	1.95	NA	NA	0.21	1.59	NA	NA

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