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Institute of Silviculture and Forest Protection in Tharandt,
Faculty of Environmental Sciences, TU Dresden

Oak regeneration ecology in managed forests: the role of silviculture

Workshop: Oak trees in conifer-dominated forests

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(1) Options and objectives of oak management and regeneration establishment

- Primary objectives for oak management

- continuous production of high quality wood
- preservation of habitat trees and restoration of conifer-dominated plantations
- esthetical function of old trees as cultural relicts

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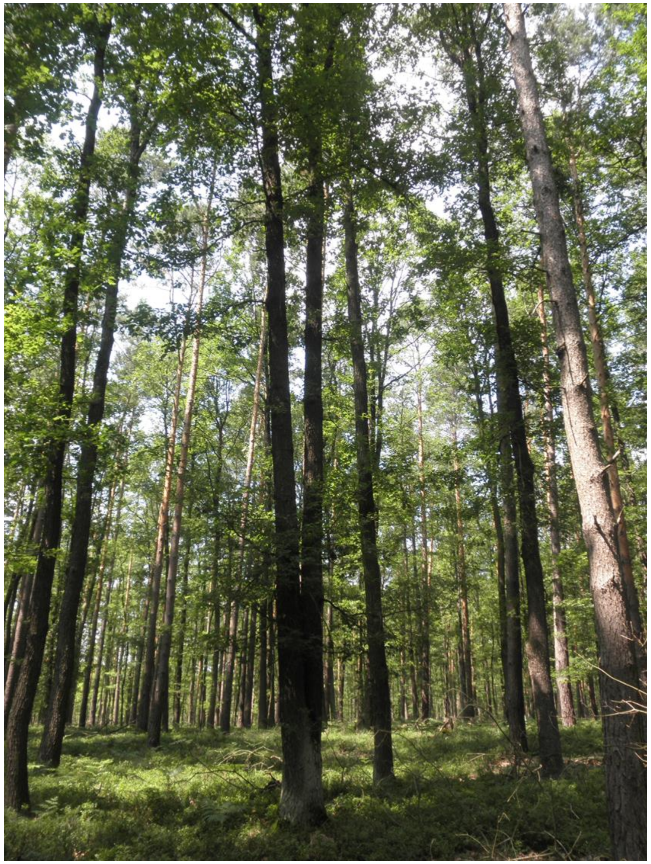
(1) Options and objectives of oak management and regeneration establishment



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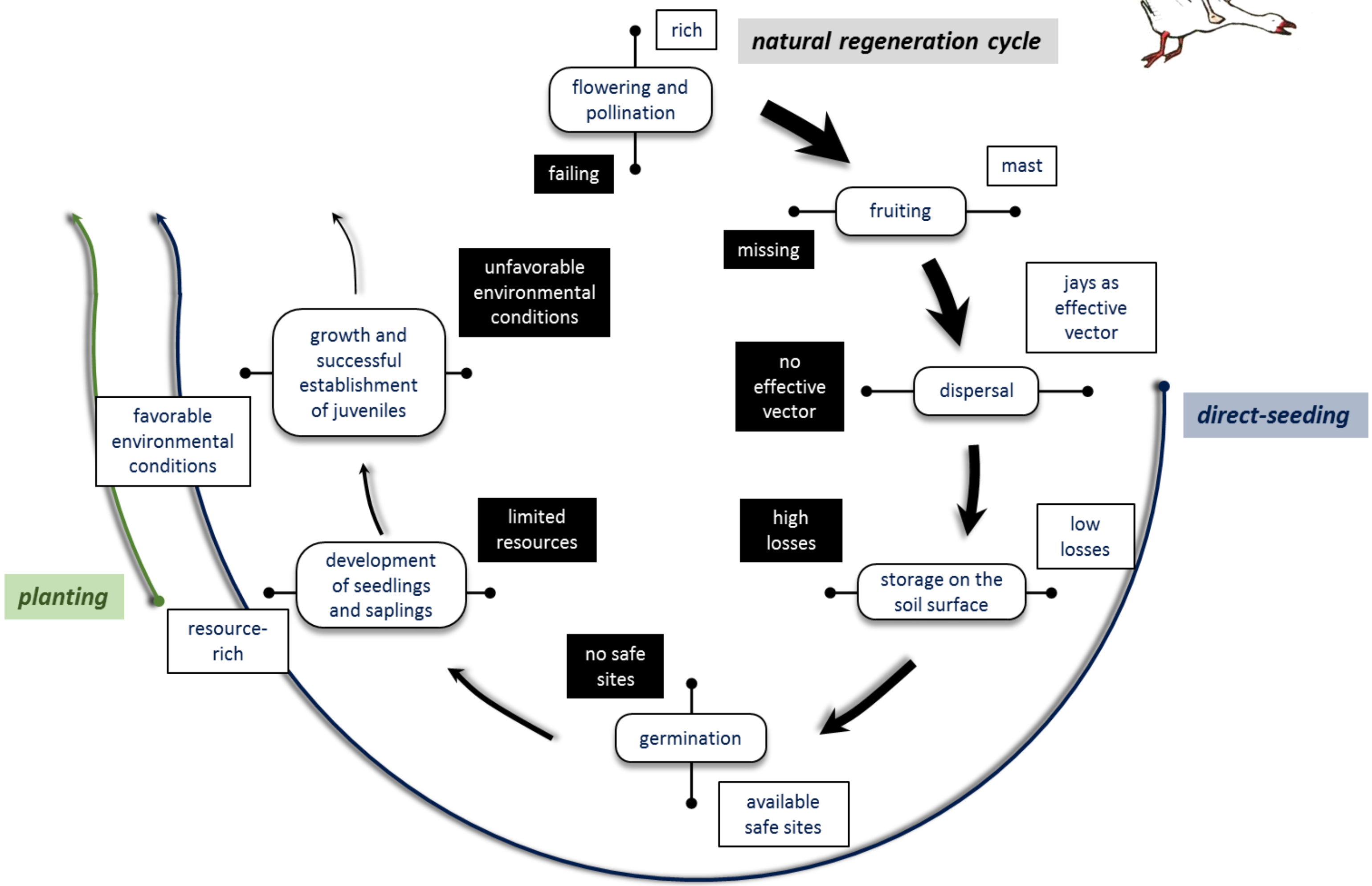
- Establishment of admixed stands

- combination of tree species pairs (shade tolerant versus light-demanding tree species)
- favourable forms of admixtures (single-tree, small up to larger groups)

- Types of regeneration establishment:

- natural regeneration
- direct seeding
- planting (nursery plants or wild seedlings)

(2) Regeneration cycle: stages and processes



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(2) Regeneration cycle

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- **Reproduction**

(Flowering, Pollination, Seed production)

- major factors of influence

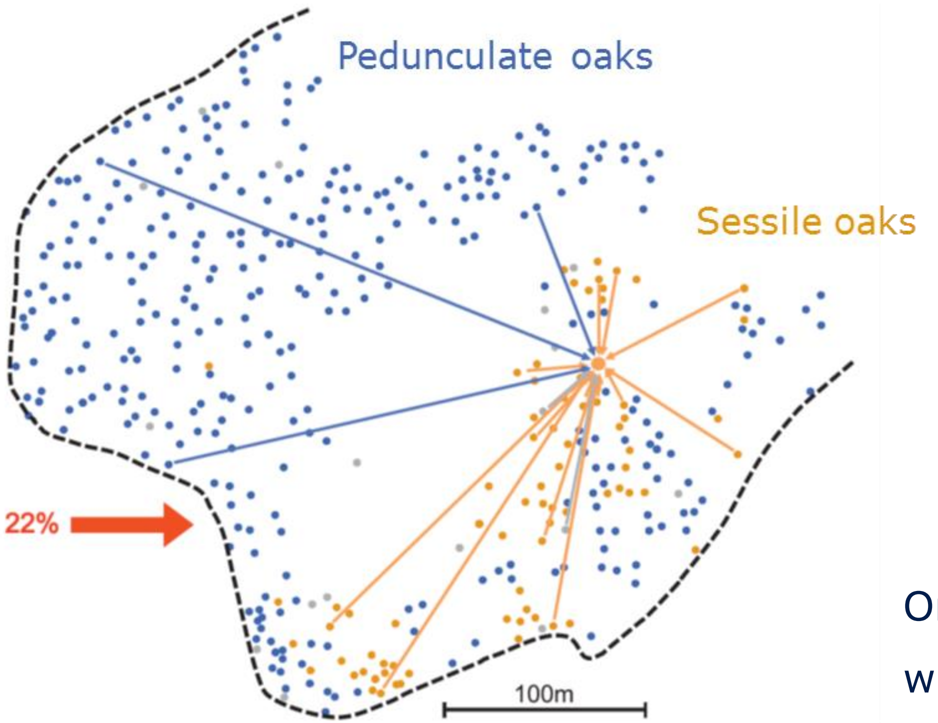
endogenous

- genetic constitution (provenances, adaptedness, adaptability)
- tree age

exogenous

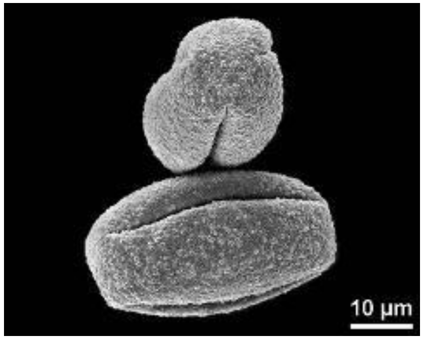
- environmental conditions (temperature, humidity)
- crown exposure and position (dominant trees)
- presence of predators or diseases

- Crown exposure and position: Pollination and flowering



Proportion of seeds produced by the adult oak were pollinated by trees outside the stand area.

Holderegger et al. (2015)



https://www.paldat.org/pub/Quercus_robur/301214

On average, the percentage of the wind-borne oak pollen from outside the stand was 60%, with large variation among stands (21–88%). (Gerber et al. 2014)

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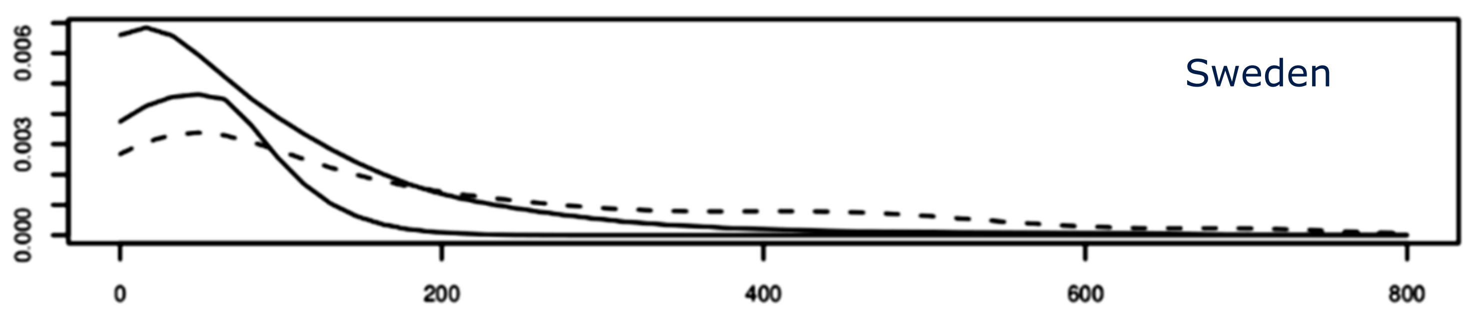
- Pollination and dispersal distances

	Pollen dispersal			
Site	**Min (m)**	**Max (m)**	***b***	**δ (m)**
France	0.0	216	0.23 (0.07–0.39)	15.6 (7.5–22.4)
Italy	0.0	836	0.14 (2.52e-06–0.28)	5371.1 (1923.4–9708.2)
The Netherlands 98	0.0	264	0.14 (0.02–0.27)	671.1 (45.6–5306)
The Netherlands 02	19.2	233	0.08 (0.007–0.29)	1101.6 (54.2–7018.6)
Spain	0.0	9977	0.31 (2.56e-20-0.47)	5149.4 (1028.5-9612.0)
Great Britain	0.0	644	0.01 (3.72e-44-0.09)	1185 (186.7–4722.9)
Denmark	0.0	224	0.23 (2.21e-14-0.53)	166.3 (61.5–603.7)
Sweden	0.0	841	0.04 (0.008–0.12)	497.1 (227.2–1969.5)
Switzerland	0.0	346	0.02 (0.01–0.03)	3674.4 (161.5–9242.7)

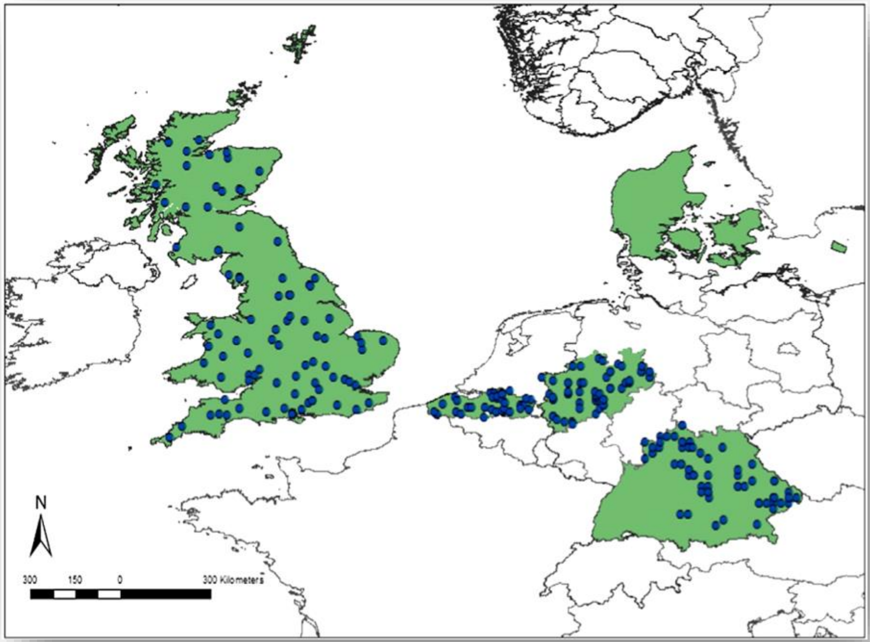


Pollen dispersal distances [m]

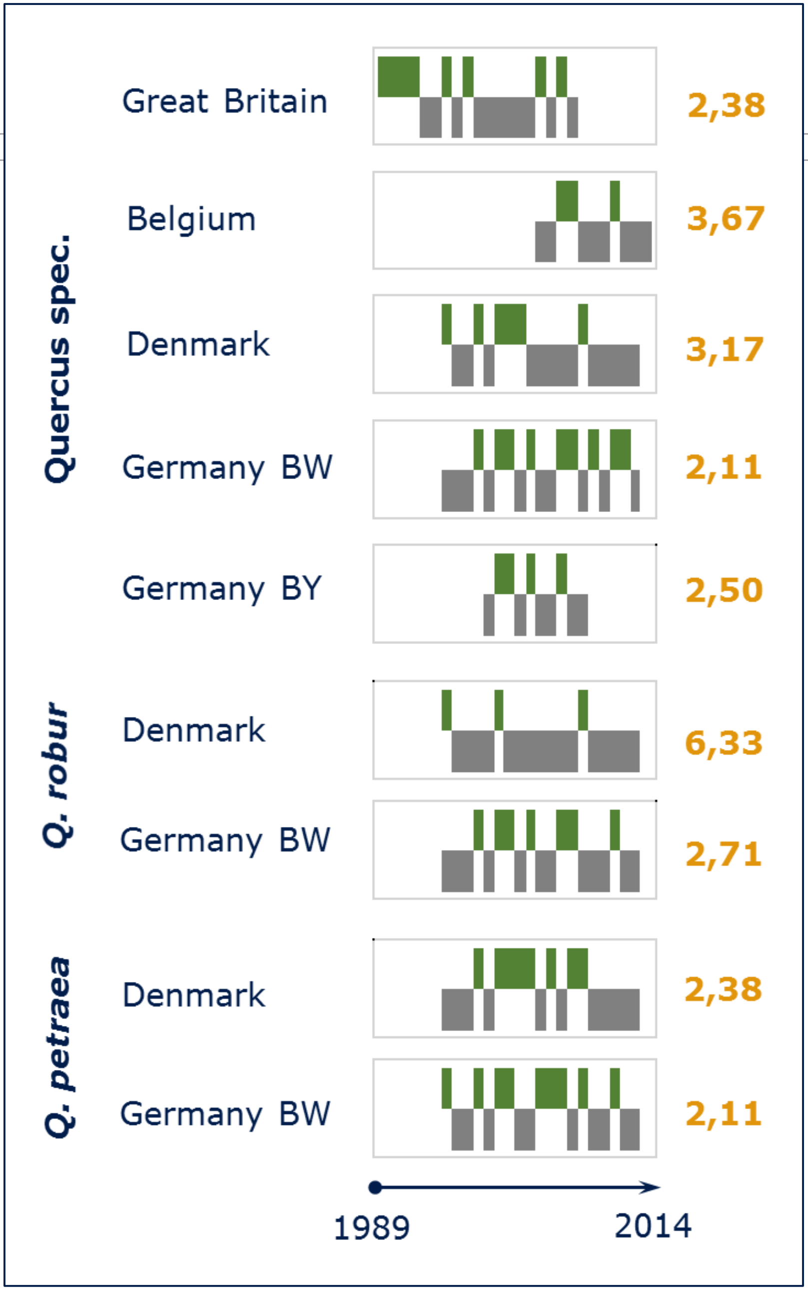
Quercus spp.
(Gerber et al. 2014)

Seed/ acorn production: mast years of Quercus spp.

Characteristics of mast-seeding (Liebhold et al. 2004): temporal variability and **relative spatial synchrony (≤ 10 km)**



Modified according to Nussbaumer et al. (2016)



green = common or abundant fruiting
grey = absent or scarce fruiting
orange = mast frequency

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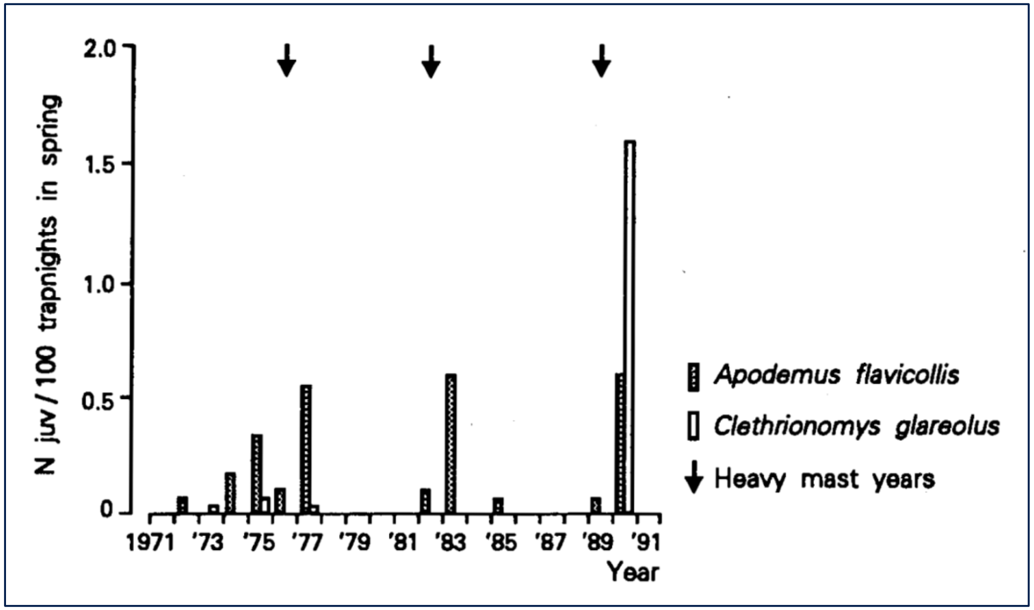
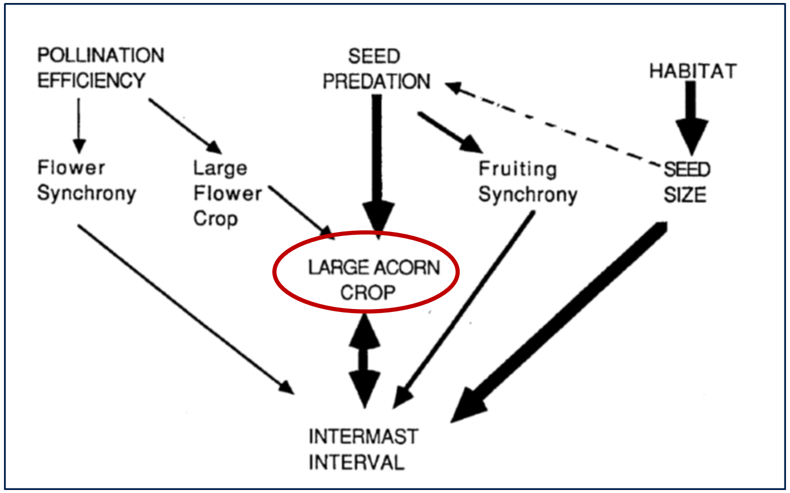
- **Seed/ acorn production: mast years of Quercus spp.**

Hypothesis: mast seeding allows survival of seeds by periodically satiating seed predators

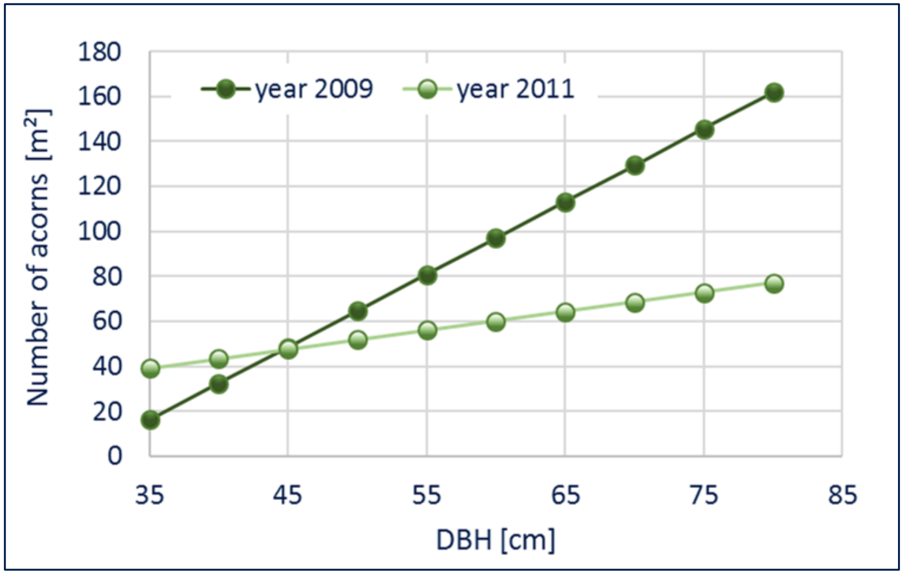


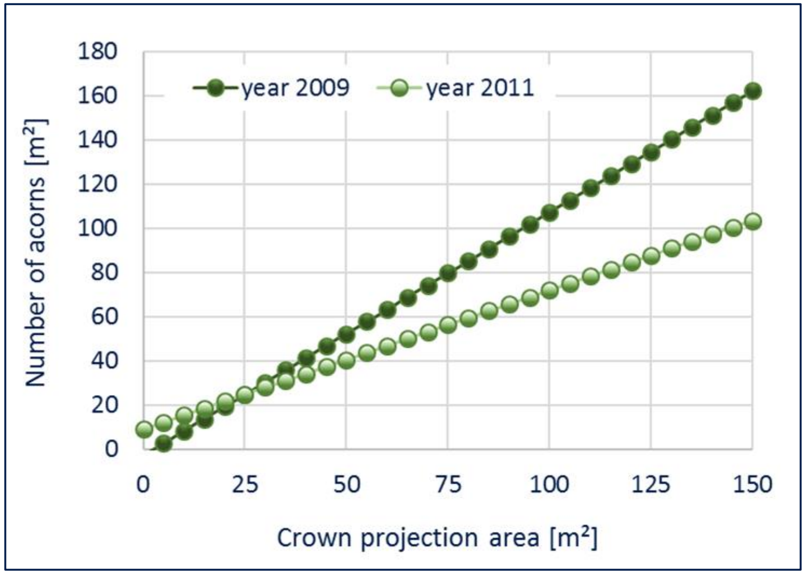
Pucek et al. (1993)



General model for the evolution of mast-fruiting in temperate deciduous oaks. (Sork 1993)

- **Crown exposure and position: Seed/ acorn production**
- allometric relations between DBH, crown dimensions and the amount of produced acorns (Gysel 1957, Bellocg 2005)
- most acorns are located in surface area of light crown
- sometimes acorn production in older stand decline with age (Dey 2014)





Martiník et al. (2014)

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(I) Interim conclusion: flowering, pollination and acorn production

- adequate spatial network of mature oaks (100 to 500 m) to ensure sufficient pollen dispersal and pollination with high fertility
- regional mast events are mainly influenced by climate, but the individual or stand specific seed production can be influenced actively
- enhancing individual tree vitality and surface area of light crown

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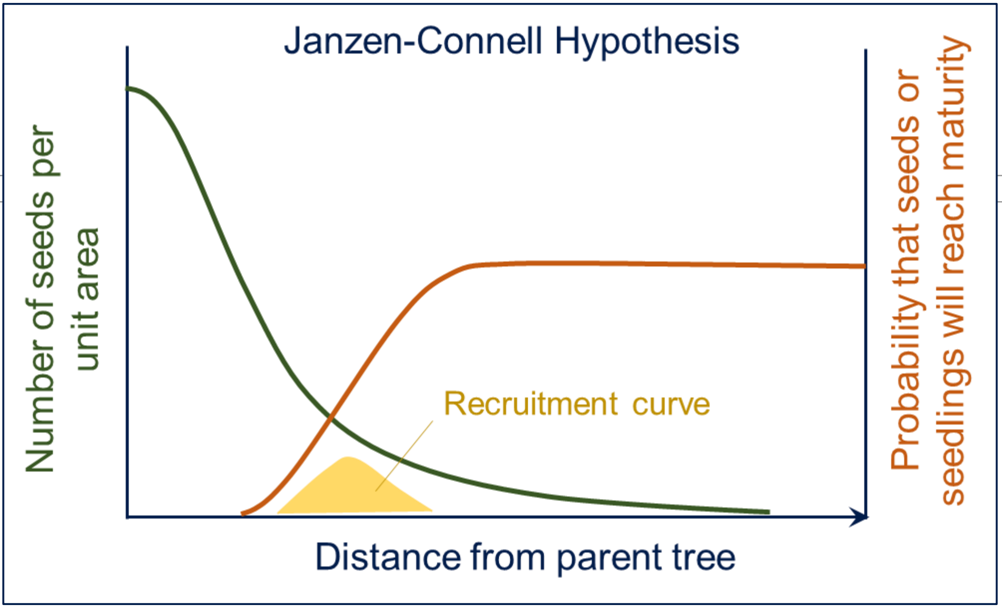
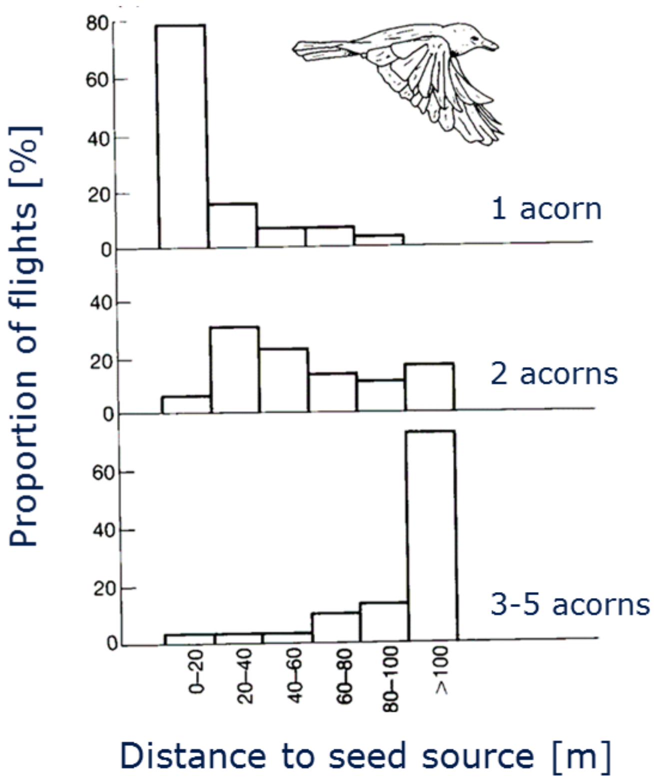


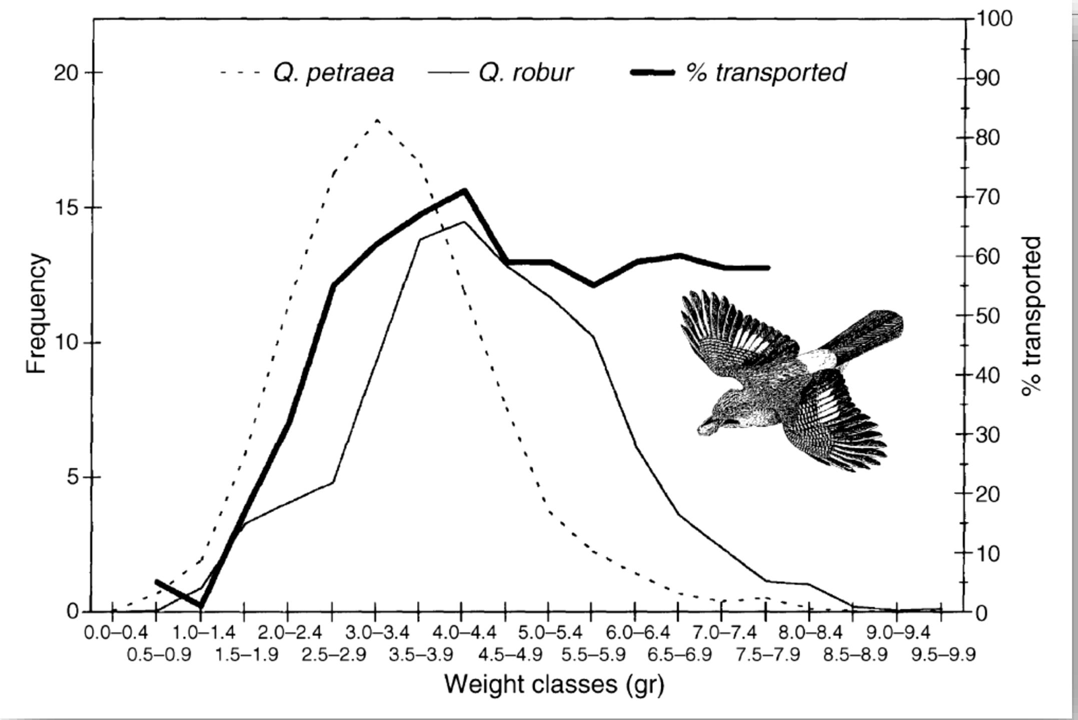
- **Seed dispersal and storage**
  - combination of barochorous and zoochorous (Eurasian jays, rodents) dispersal mechanisms



(Bossema 1979)

- detailed information about the Eurasian jay as main dispersal driver
- 1 to 5 breeding pairs per 1km² (Keve 1985, Gómez 2003)
- always movement of acorns from seed source (up to 13 flights/ hour) (Turček 1961)

- **Seed dispersal and storage**
  - preferred places for caches (**landscape**)
    - open Pine forests with low height of ground vegetation
    - along forest tracks
    - outside oak stands
    - avoidance of complete open sites



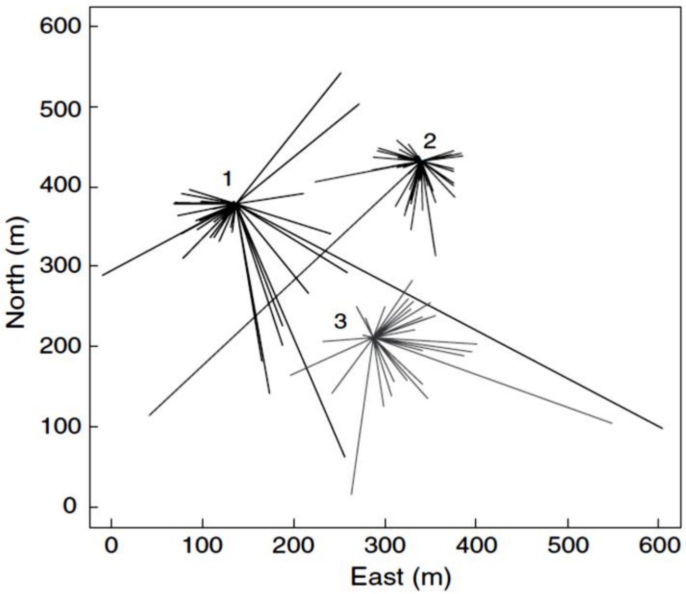
Selection of acorns by jays according to weight, showing that acorns of *Q. robur* will be preferentially collected by the bird, as their size better match its preferences. (after: Bossema, 1979; Dupouey & Le Bouler, 1989)

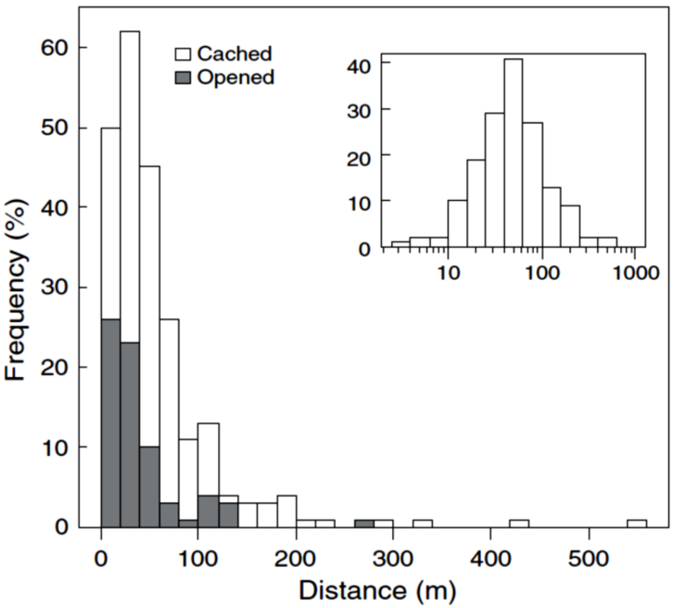
- preferred places for caches (**micro-habitats**)
  - close to pine trunks, rocks and other landmarks
  - understorey layer with sparse ground cover
  - tall shrubs

Eurasian jay (*Garrulus glandarius*), Photo: Duncan Usher/ Minden Pictures/National Geographic Creative

- **Seed dispersal and storage**

○ combination of near = barochorous + rodents (± crown radius) and long-distance dispersal = jays (> 10 m up to 1 km) (Scofield et al. 2010)





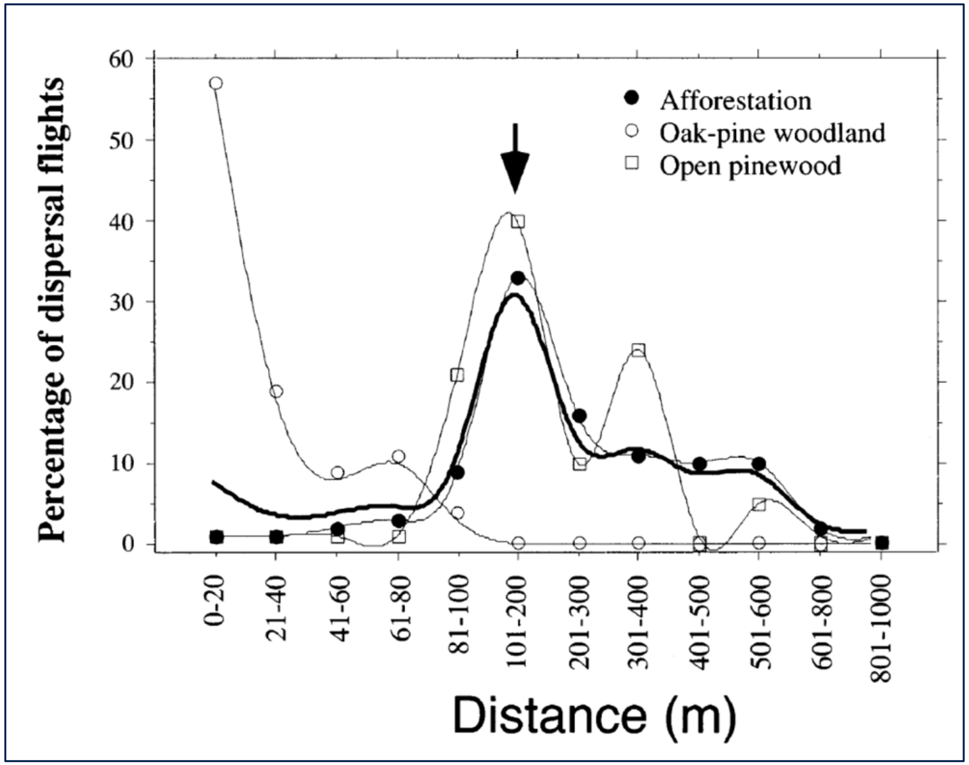
Dispersal experiment with feeders (Pons & Pausas 2007)

○ **Mean dispersal distances**: 68 m (values between 3 to 550 m; Pons & Pausas 2007)

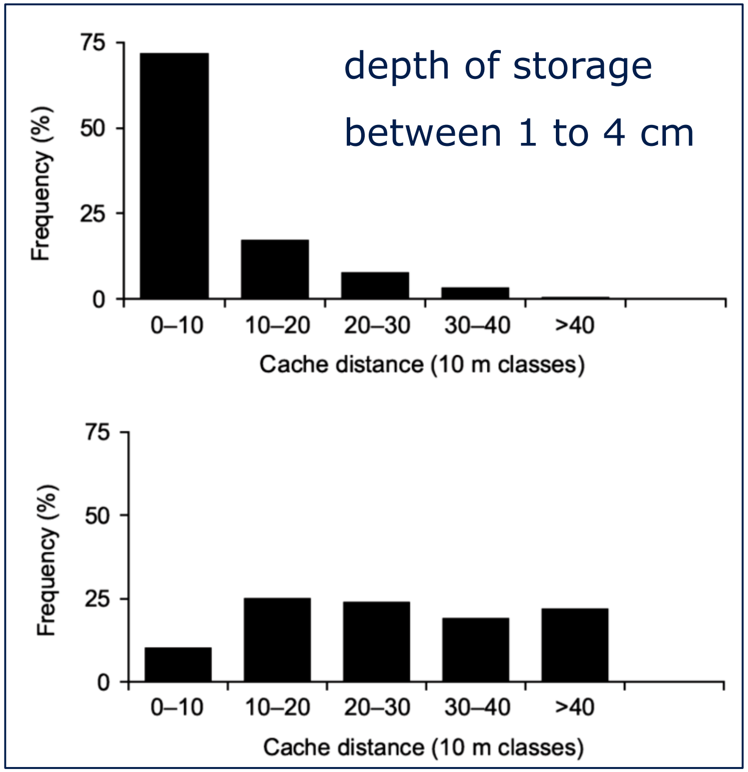
263 m (values between 5 to 1000 m; Gómez 2003)

Photo:
Matthieu Berroneau

- **Seed dispersal and storage**
  - long distance-dispersal depends on surrounding landscape structure



Disperal of *Quercus ilex* by **jay** (Gómez 2003)

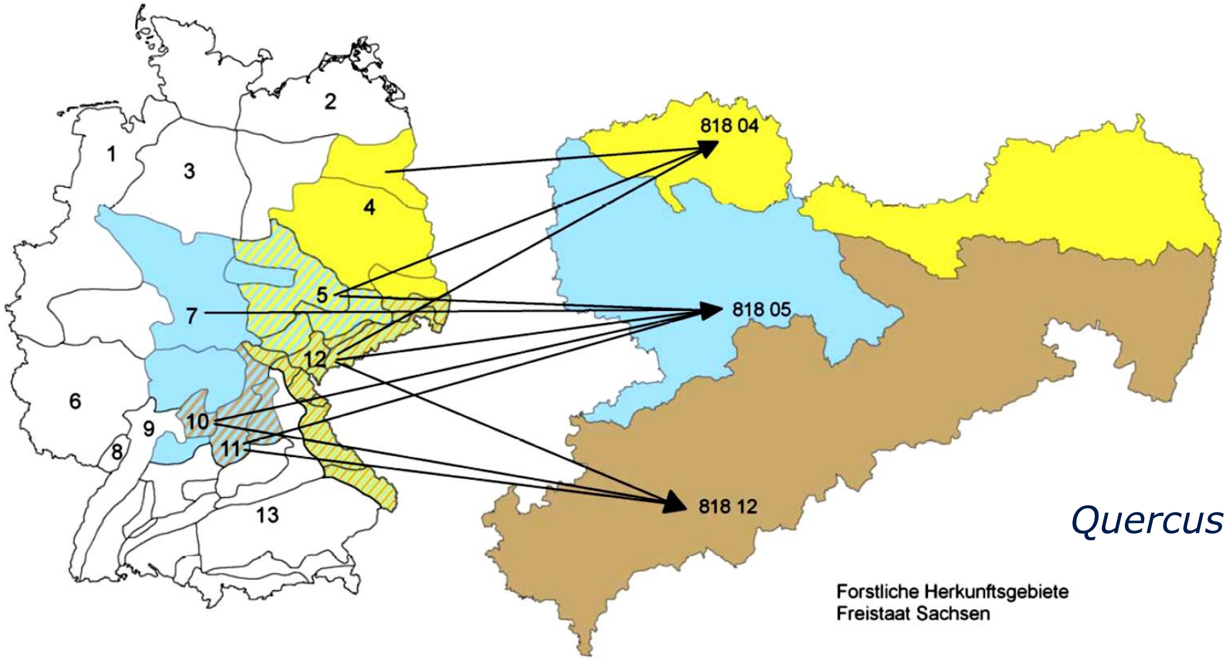


Dispersal of *Quercus petraea/ robur* by wood mice (Ouden 2000)

→ Seed dispersal and storage

direct seeding

- distribution of acorns or plants disentangled from local or regional sources are possible (landscape scale) = regulated by recommendations for provenances



- sources are seed orchards or approved forest seed stands

Quercus petraea (Saxony)

- optimization of seed storage (2 years), temperature – 4°C °C, seed water content appr. 40 – 45 %

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(II) Interim conclusion: seed dispersal and storage

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- early, continuous thinnings and competition regulations in favour of oak trees to keep them in the dominant overstorey crown layer
- protection of suitable habitat conditions for jays as main and effective acorn dispersal vector
- adequate spatial network of mature oaks (≤ 100 to 200 m) to ensure adequate seed densities
- additional establishment of seed boxes in areas without mature oak seed trees

→ germination: survival rates, substrate, main factors of influence

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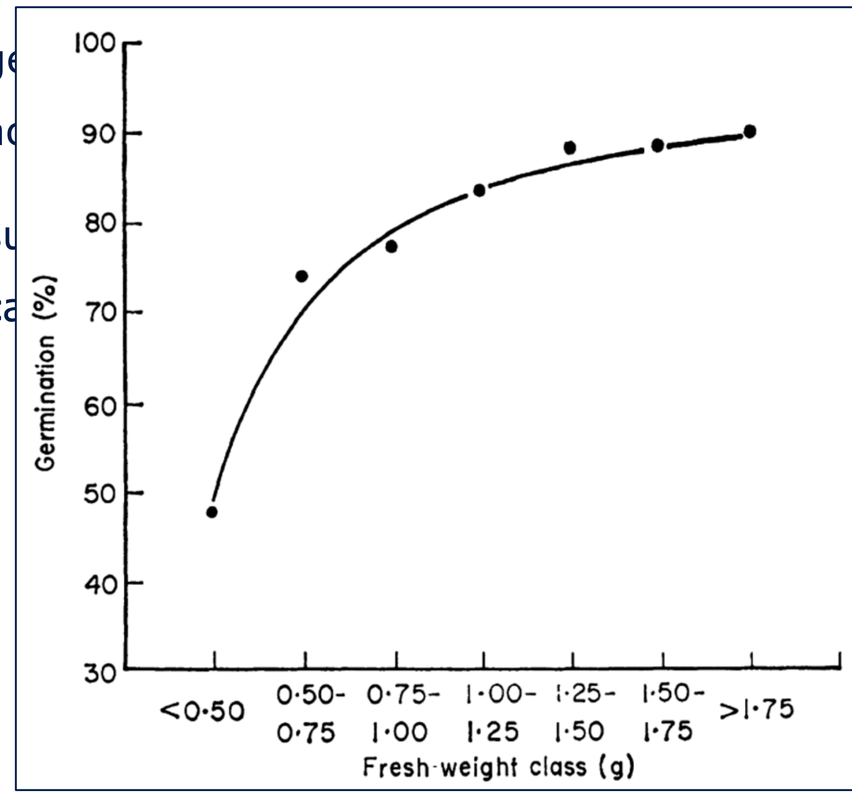
hypogeal germination
('below ground')

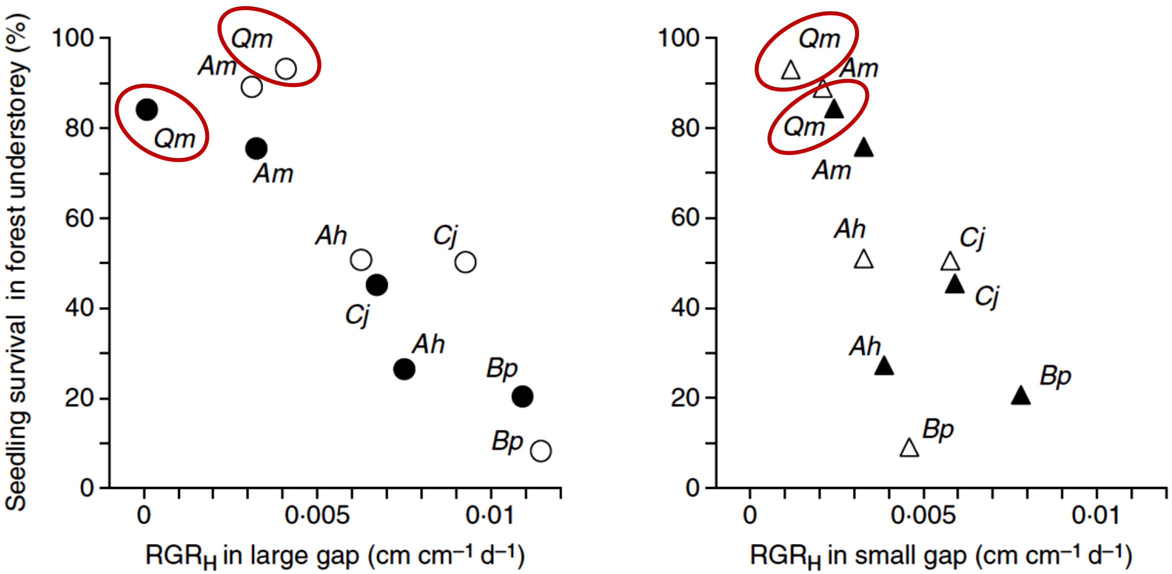
Acorn size and fresh weight significantly affects germination percentages and germination rates (i.a., Shaw 1968, Tilki 2010)

→ natural regeneration and direct seeding

- oak as an example of acorns are desiccation and frost damage sensitive
- ge … end on ac
- su … ditions ca … s



→ germination: survival rates, substrate, main factors of influence



Seiwa 2005 (1year old *Q. mongolica* seedlings)

- ○ main risks and problems for this development stage
- \- drought period during spring time
- \- damages by browsing
- \- missing radicle contact to the mineral soil
- \- damages caused by frosts and rodents

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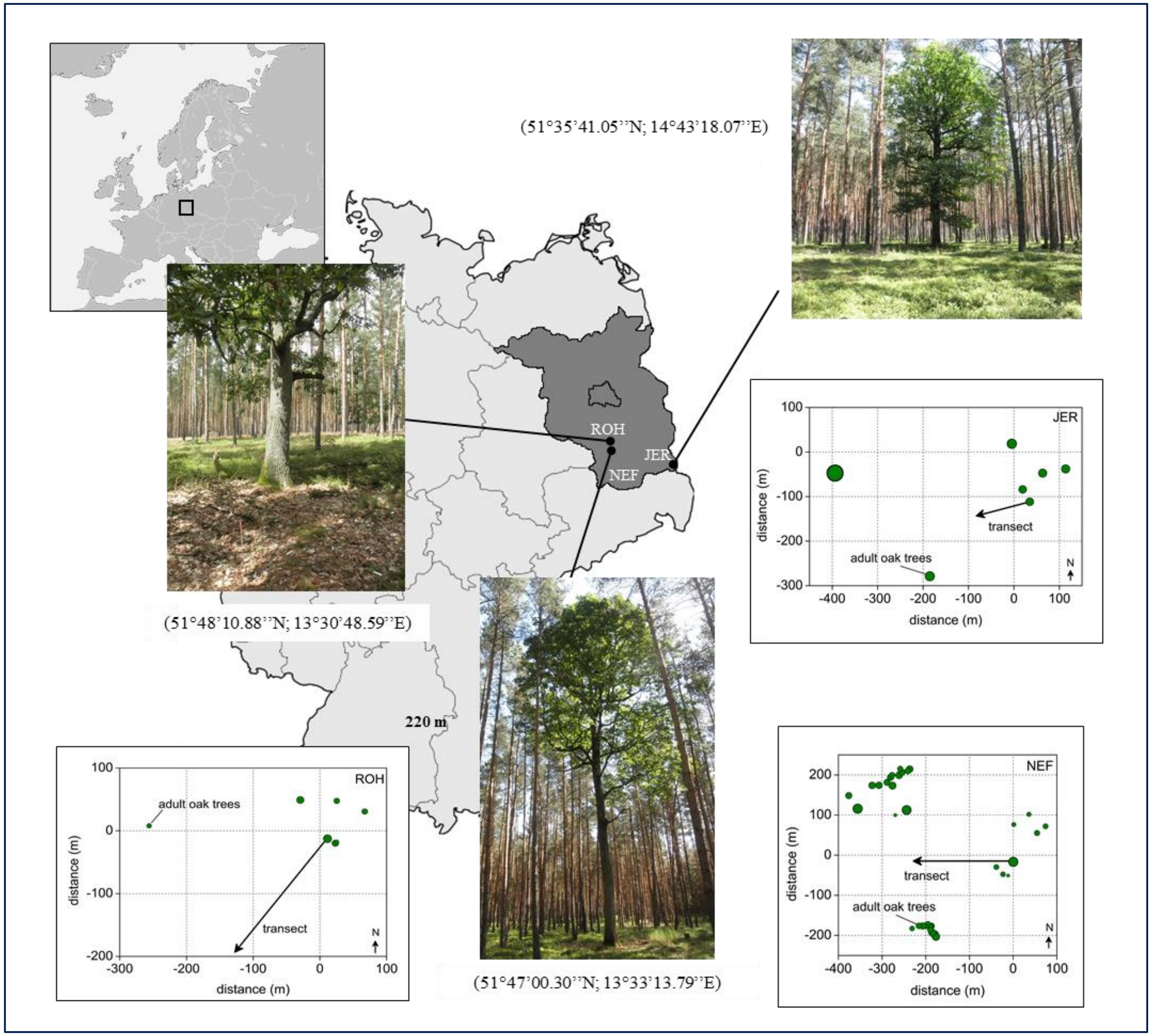
→ Seedlings and saplings: oak density

Density of **natural regeneration** established by jays within Scots pine forests

Source	Number of oak seedlings [ha]	Location
Janitschek (1987)	3.000 - 3.500	Lower Saxony
Steiger (1987)	7.200 - 14.600	Lower Saxony
Heidmeier (1988)	451 - 3.900	North Rhine-Westphalia
Hendriks (1990)	1.007	Lower Saxony
Horst (1990)	205 - 2.305	Lower Saxony
Leder (1993)	492	North Rhine-Westphalia
Schmidtke (1993)	610 - 988	Lower Saxony
Böllet (1994)	1.984	Bavaria
Borys (1998)	1.200 - 6.266	Brandenburg
Mosandl & Kleinert (1998)	2.000 - 4.255	Saxony
Schirmer et al. (1999)	≤ 5.573	Bavaria
Schuppert (1999)	645 - 2.888	Brandenburg, Berlin
Stimm (1999)	77 - 624	Bavaria
Stähr & Peters (2004)	< 2 m height up to 40.000, > 2 m height 370 - 1.810	Brandenburg

(modified according to Stimm & Knoke 2004)

Seedlings and saplings: Density combined with spatial aspects



Stand characteristics:

- age of pine 50 to 87 years
- age of oaks > 150 to 200 years
- number of adult oak trees within a radius of 250 m: JER 7, NEF 35 and ROH 7

Methods:

- transects starting from parent oak tree
- length up to 220 m x width 5 m

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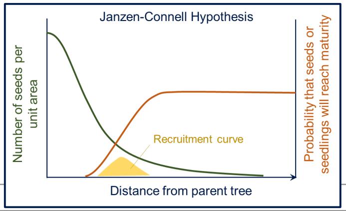
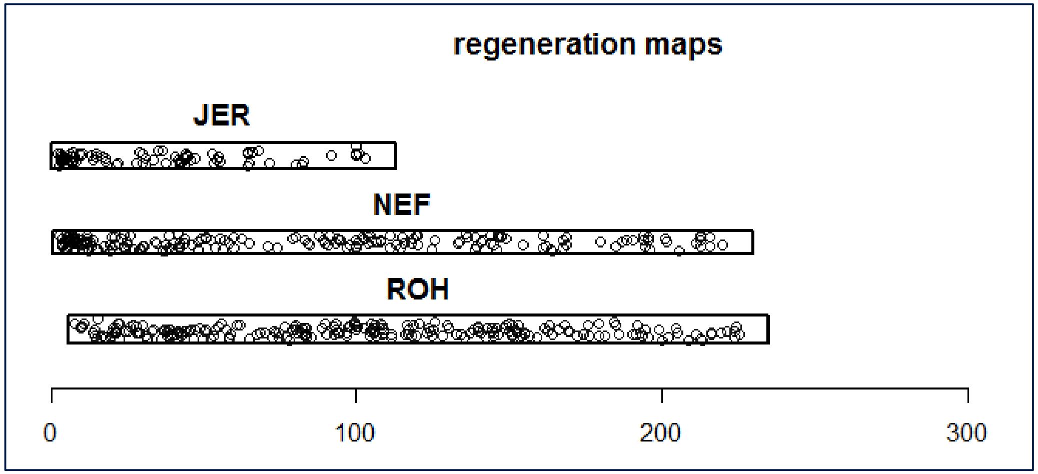
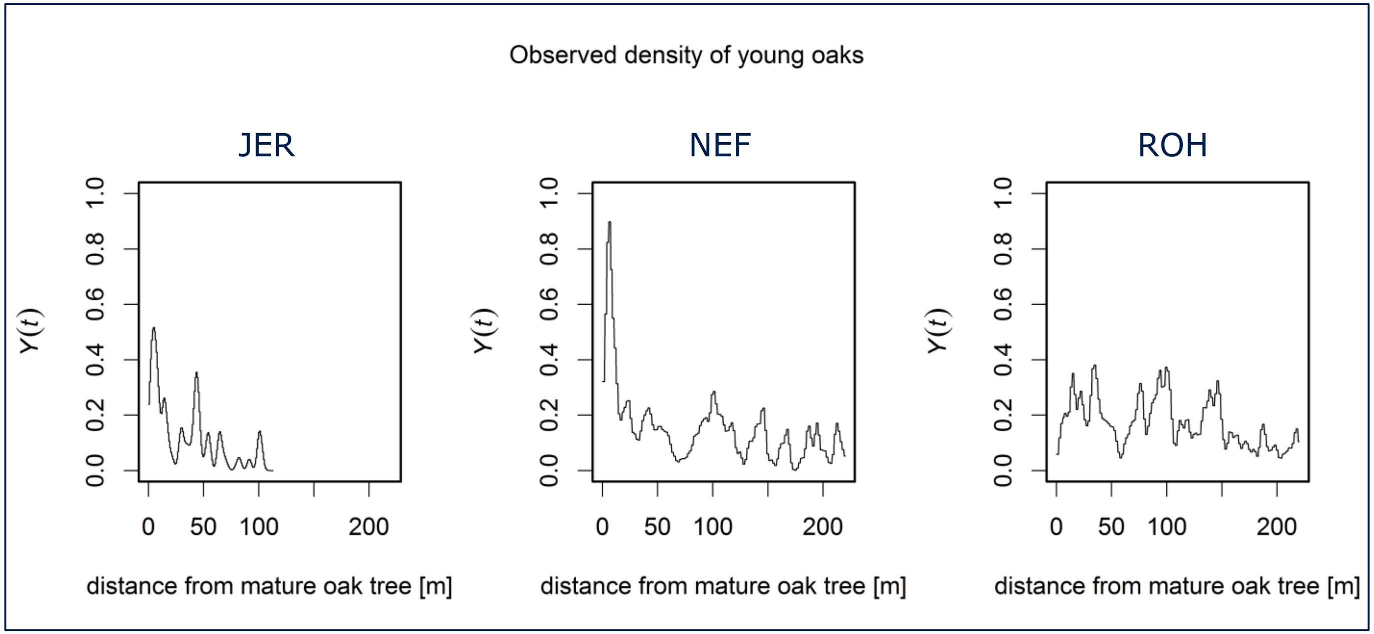


→ Seedlings and saplings: Spatial scale on stand level





(Huth et al. *in prep.*)

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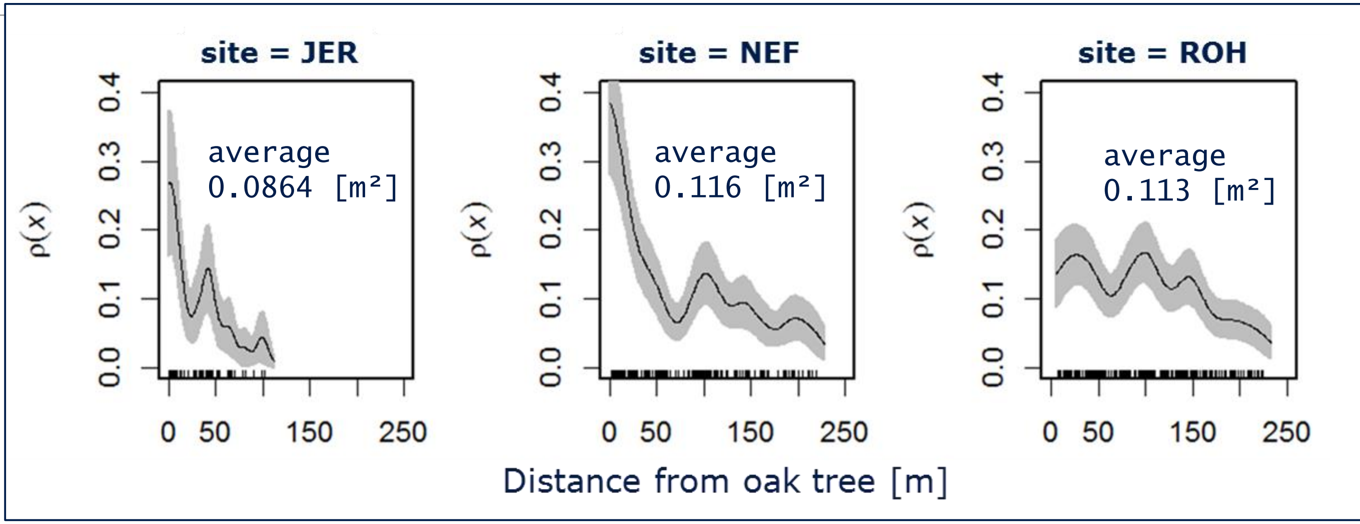
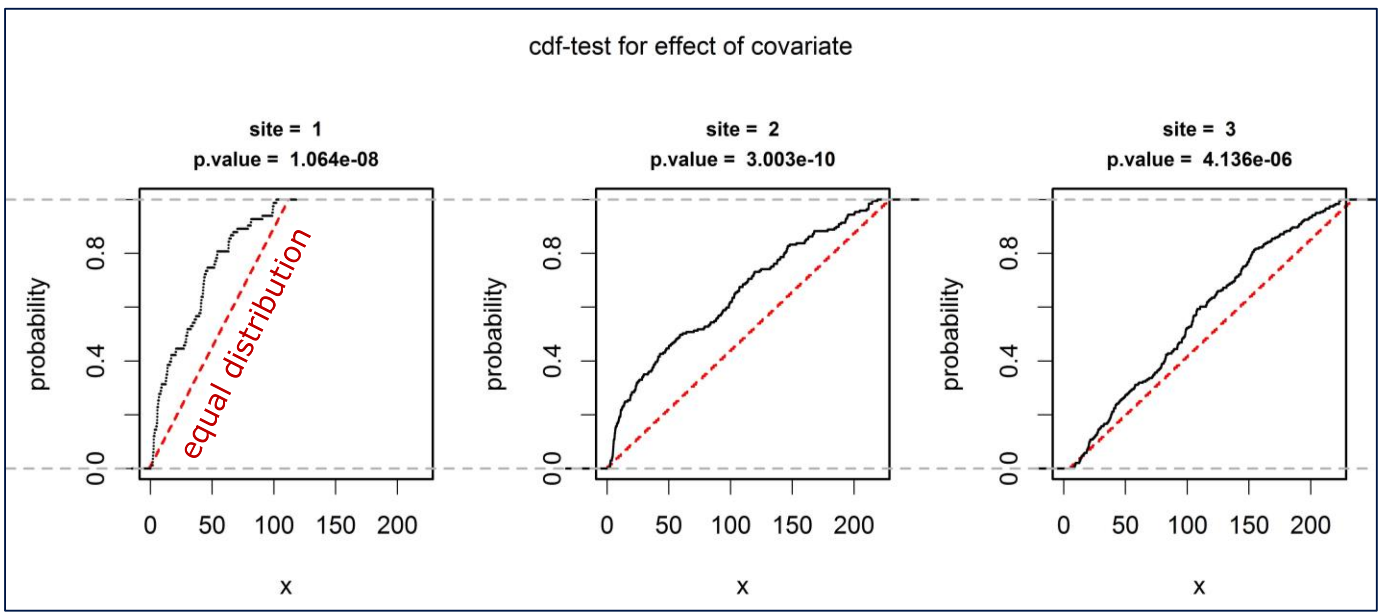
→ Seedlings and saplings: Spatial scale on stand level





- → point pattern analyses (combination of factors, covariates, interactions, coordinates)
- → cdf-test = spatial distribution test for point pattern or point process model
- → comparison between observed and predicted (poisson) distribution of oak seedlings (i.a. Baddeley et al. 2005)

(Huth et al. *in prep*.)

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→ Seedlings and saplings: development

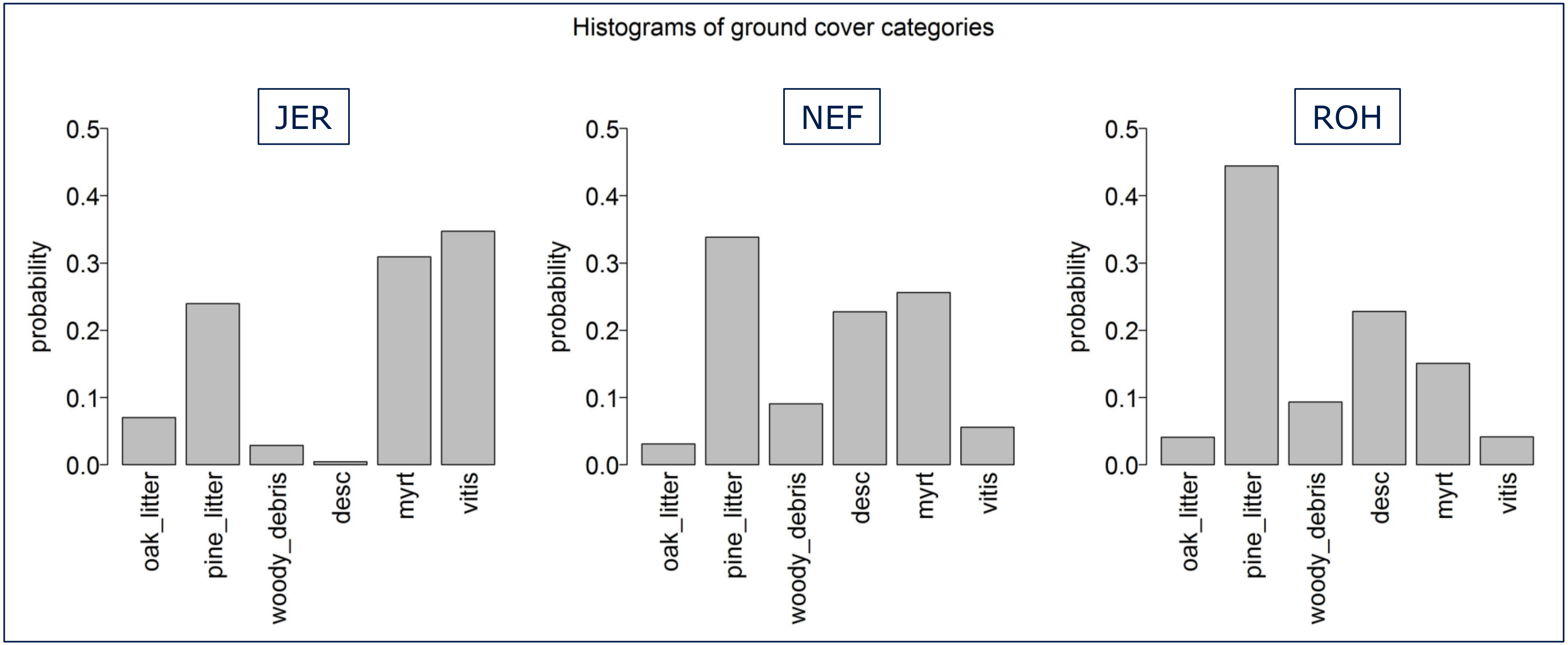
important aspects	natural regeneration, direct seeding and advanced planting
desired/ targeted number of individuals [ha]	**minimum** of 7.000 to 10.000 (up to 15.000) oaks [ha] to get trees with good qualities (Noack 2004)
influence of coniferous shelter trees	older saplings = significant decrease of oak density, height and dbh growth caused by Scots pine shelter compared to open areas; but ground cover and frost damages are also reduced (Löf 2000, Stähr & Peters 2000)
light dependent growth	increase of light requirement with increasing **age** and **size of regenerated oaks** (Farque et al. 2001, Löf & Welander 2004, Annighöfer et al. 2016); **minimum** of available light 10 to 12 % (Jarvis 1964, Dobrowolska 2006); **optimal light** level 25 to 50 % RLI caused by an optimized micro-climate (Jarvis 1964, Ziegenhagen 1989, v. Lüpke 1995, Hauskeller-Bullerjahrn 1997, Löf et al. 1998, Ammer 2003, Löf et al. 2007, Březina & Dobrovolny 2011, Götmark et al. 2011); **light quality** (Ammer 2003, Vernay et al. 2016) **survival probability** under closed shelter ≤ 3 years (Mosandl & Kleinert 1998)
nutrients and pH-value	low levels of available nutrients (N, P, K, Ca, Mg, Fe) cause effects on height growth, number of internodes, leave mass, root collar diameter and root development (Ovington & MacRae 1960, Collet et al. 1997, Mirschel et al. 2011, Vernay et al. 2016)

→ Seedlings and saplings: development

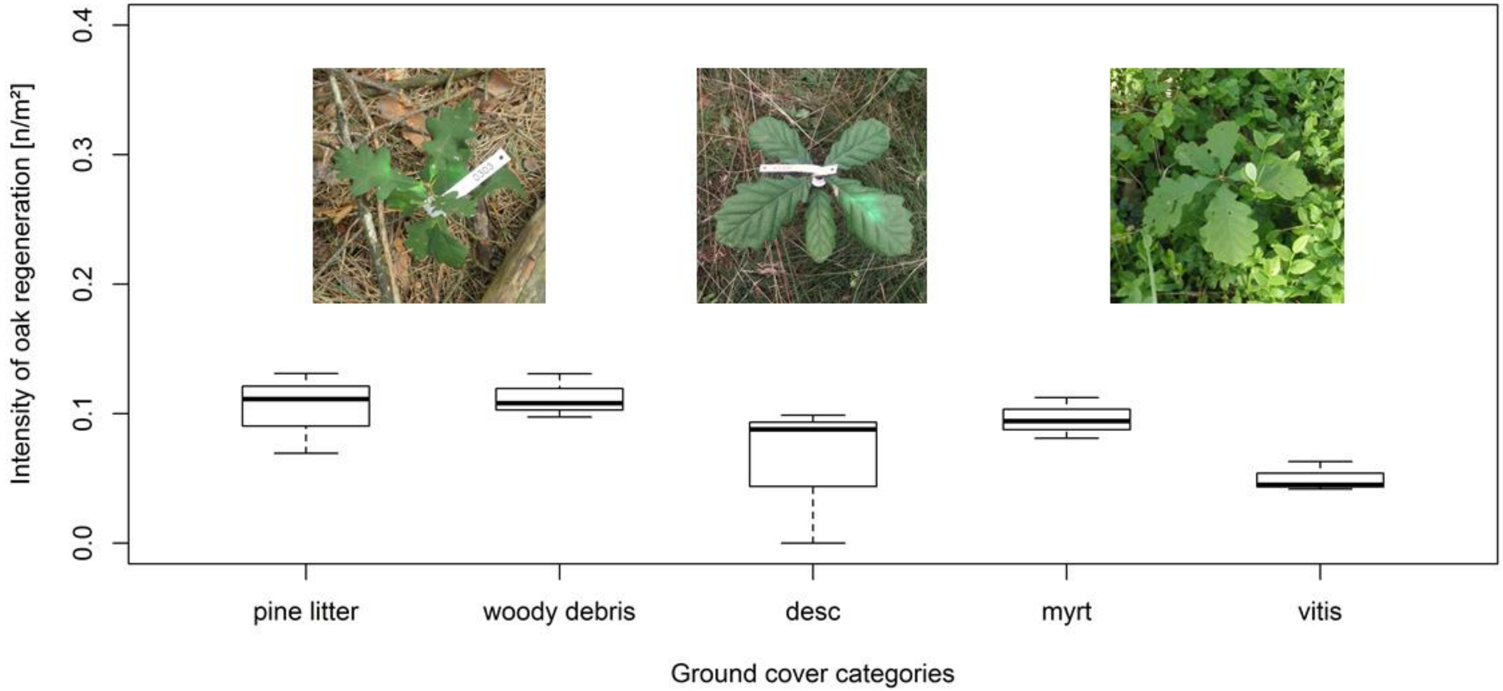
important aspects	natural regeneration, direct seeding and advanced planting
water availability	water balance and availability of the upper soil layer affect seedling density, above- and below-biomass (Löf & Welander 2004, Beon & Bartsch 2003, Rodríguez-Calcerrada et al. 2010, Mirschel et al. 2011, Kuster et al. 2013);
browsing	negative effects especially for oaks between 50 cm and 130 cm in height (Löf 2000, Dobrowolska 2006, Götmark et al. 2011, Jensen 2011, Annighöfer et al. 2015)
interspecific competition	effects of different **ground vegetation types** → **moss**: (+) Mirschel et al. (2011) **grasses**: (+/- to -) Ovington & MacRae (1960), Lorimer et al. (1994), Collet et al. (1996), Harmer & Morgan (2007), Vernay et al. (2016) **herbs**: (+) Mirschel et al. (2011) **shrubs**: (+/- to -) Ovington & MacRae (1960), Harmer & Morgan (2007), Götmark et al. (2011) **bracken/fern**: (+/- to -) George & Bazzaz (1999), Harmer & Morgan (2007) seedlings and saplings of **other tree species** → **deciduous** tree species: (+/- to -) beech (Harmer & Morgan 2007, Annighöfer et al. 2015); (+/-) hornbeam; lime & sycamore (-) (Dobrowolska 2006) **coniferous** tree species: (-) spruce (Brown 1992, Götmark et al. 2011) (+/-) pine (Dobrowolska 2006, Sánchez-Gómez et al. 2006, Beon & Bartsch 2003)

→ Seedlings and saplings: Density, spatial distribution and ground vegetation

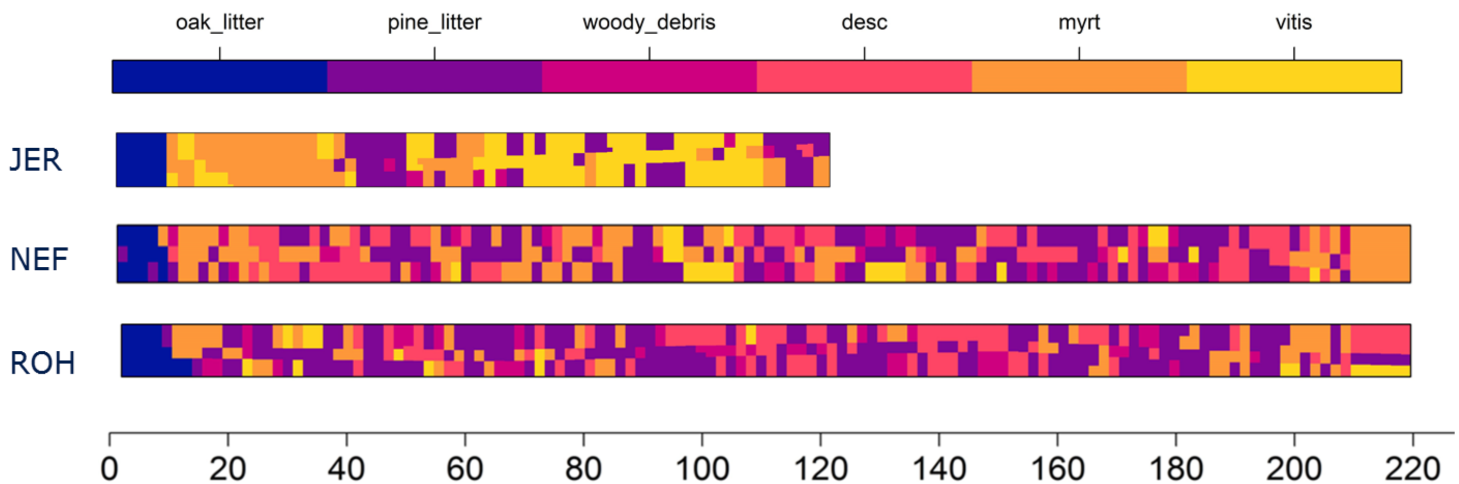
- ground vegetation as main filter influences the regeneration success



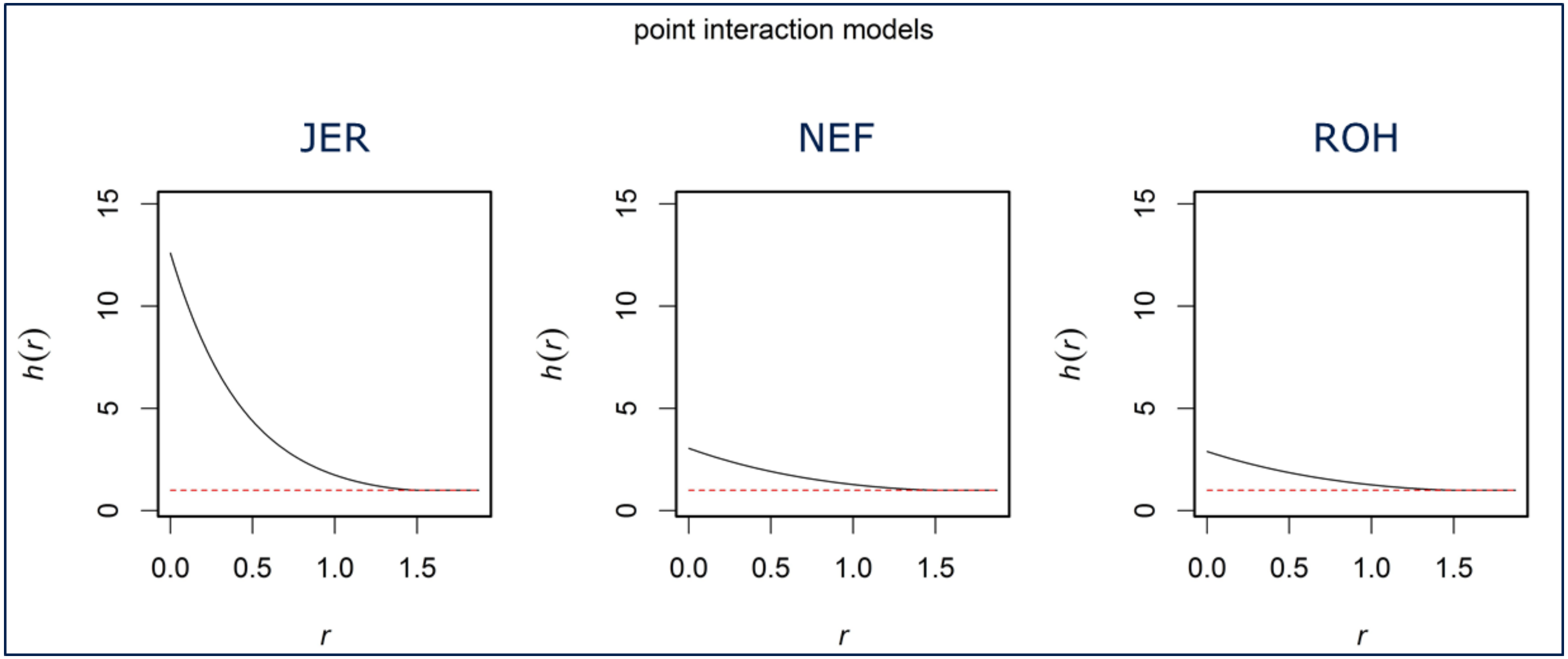
(Huth et al. *in prep*.)



- spatial mosaics of ground cover classes



(Huth et al. *in prep.*)



- distances between oak seedlings show a clustered or aggregated distribution of seedlings in distances < 1m
- distribution characteristics seem to be site-dependent

- adjust the model from distance effect caused by parent trees
- clusters of seedlings can be integrated as positive interaction

(Huth et al. *in prep*.)

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- model function to explain small-scale distribution (interaction radius 0.75 m) of oak regeneration

Coefficients	Estimate	Std. Error	t value	Pr(>|t|)	
oak_litter	-1.661e+00	3.709e-01	-4.478	7.85e-06	***
pine_litter	-2.102e+00	4.449e-01	-4.724	2.43e-06	***
woody_debris	-1.799e+00	4.886e-01	-3.682	0.000236	***
desc	-2.316e+00	4.603e-01	-5.032	5.16e-07	***
myrt	-2.293e+00	4.202e-01	-5.458	5.23e-08	***
vitis	-2.527e+00	5.221e-01	-4.841	1.36e-06	***
x_distance	-9.564e-03	1.840e-02	-0.520	0.603328	
I(x^2)	-4.522e-05	1.884e-04	-0.240	0.810353	
Standort2	8.114e-01	4.728e-01	1.716	0.086242	.
Standort3	-1.855e-01	4.685e-01	-0.396	0.692106	
Interaction	2.275e+00	4.530e-01	5.023	5.41e-07	***
x:Standort2	-1.408e-03	1.814e-02	-0.078	0.938131	
x:Standort3	1.918e-02	1.823e-02	1.052	0.292999	
I(x^2):Standort2	6.693e-05	1.867e-04	0.358	0.720024	
I(x^2):Standort3	-9.557e-06	1.870e-04	-0.051	0.959235	
Standort2:Interaction	-1.378e+00	5.596e-01	-2.463	0.013823	*
Standort3:Interaction	-1.262e+00	5.215e-01	-2.420	0.015574	*

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

explanation of small-scale distribution by ground cover

→ no sign. influence of distance from parent tree

→ effects of effect of interactions between seedlings

→ site specific interaction between seedlings

Area-interaction process, Disc radius 0.75
Interaction 1:
Fitted interaction parameter eta: 9.8554
Interaction 2:
Fitted interaction parameter eta: 2.4492
Interaction 3:
Fitted interaction parameter eta: 2.7829

→ cdf-test by Monte Carlo method of the model fitted to multiple point patterns (p.value = 0.89)

(Huth et al. *in prep*.)

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(III) Interim conclusion

- to produce prospective high oak qualities minimum density of oak seedlings 7.000 per ha
- distance-dependent and limited regeneration densities emphasize the necessity of spatial networks of adult oaks

→ but:

- site-specific factors of influence are highly complex
- spatial analysis must be done on two different scales to explain the distribution of oak seedlings/saplings

(3) Creation of admixtures with coniferous tree species

- **Why do we know so little about such admixtures in their juvenile development stages?** (Cannell et al. 1992)

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- often low densities of regenerated oaks

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(3) Creation of admixtures with coniferous tree species

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- most established admixed oak-pine structures are still younger than 20 years caused by forest conversion activities and deer management
- oak-spruce stands are rather rare in central Europe (Tjoelker et al. 2007)

→ possible combinations of oak and coniferous tree species

– Scots pine,

– Norway spruce,

– European larch,

– Douglas fir

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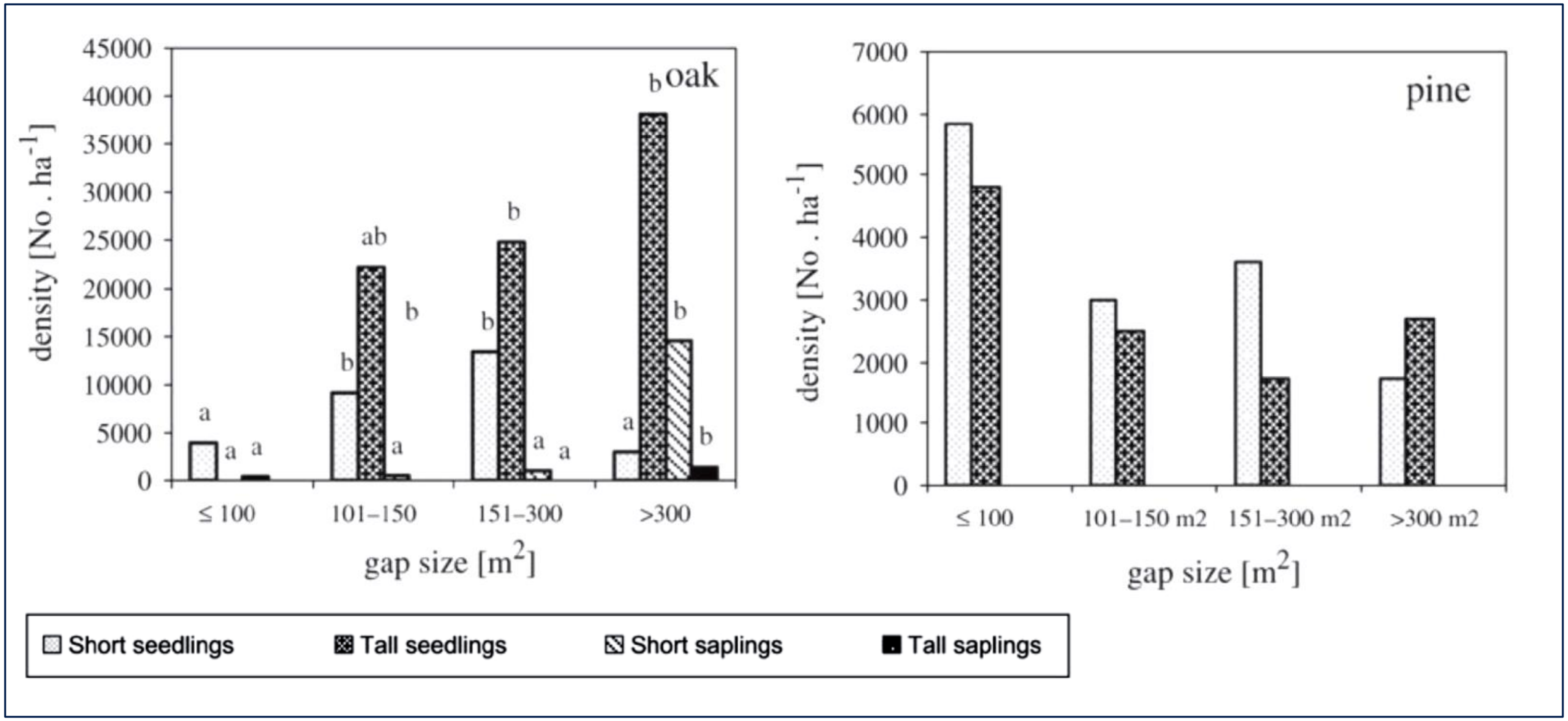
→ Established silvicultural knowledge and consequential measures

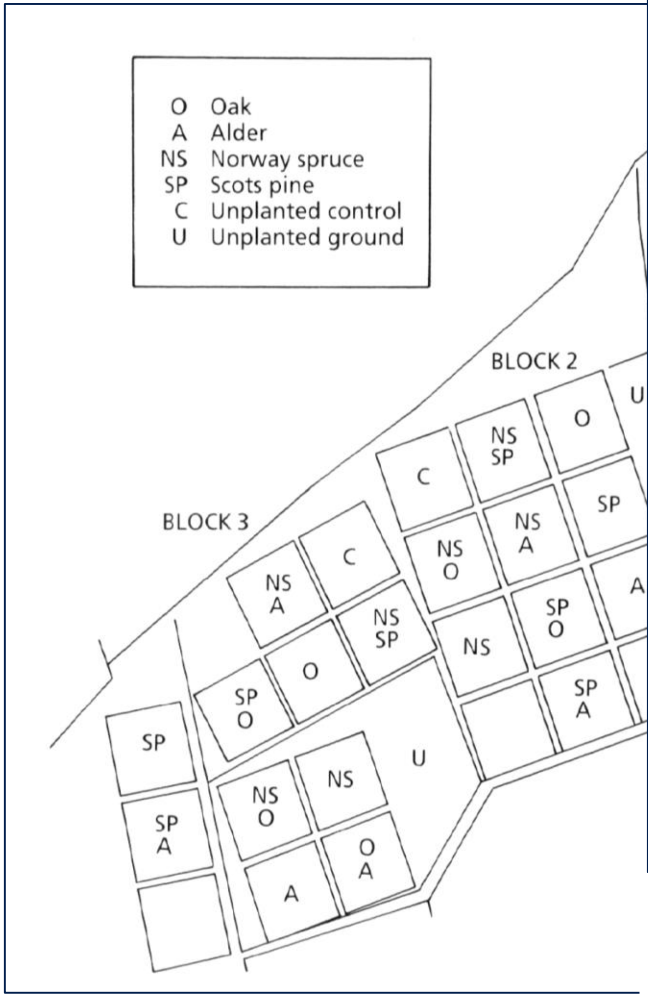
- using natural small-scale disturbances or creating gaps to establish natural or artificial regeneration of oak and coniferous tree species



- gap size decides about the light regime and the probability of establishment and growth of oaks older 1 year (i.a. Dobrowolska 2006)

(3) Creation of admixtures with coniferous tree species

- Methodical aspects – perspective of scientists



Species	Age	When admixed with: NS	Oak	Alder	SP
Norway spruce (NS)	4*	*0.48*	0.42	0.45	0.46
	7	*1.20*^{a}	1.04^{b}	1.13^{abc}	1.18^{ac}
	10	*1.86*^{a}	1.52^{b}	1.73^{ac}	2.19^{d}
	20	*5.87*^{a}	5.29^{b}	6.22^{ac}	7.11^{d}
	26	*8.80*^{a}	8.76^{ab}	9.84^{c}	10.62^{d}
Sessile oak	4*	0.33	*0.39*	0.31	0.37
	7	1.17^{a}	*1.48*^{b}	1.18^{a}	1.53^{b}
	10	1.73^{a}	*2.05*^{b}	1.88^{ab}	2.53^{c}
	20	3.63^{a}	*4.21*^{b}	4.47^{b}	6.19^{c}
	26	5.67^{a}	*6.58*^{b}	7.29^{c}	8.82^{d}
Common alder	4*	0.63	0.63	*0.63*	0.62
	7	1.56	1.56	*1.67*	1.68
	10	2.29^{a}	2.35^{ab}	*2.46*^{bc}	2.58^{c}
	20	4.90^{a}	4.99^{ab}	*5.77*^{c}	6.54^{d}
	26	7.57^{a}	7.72^{ab}	*8.24*^{c}	9.31^{d}
Scots pine (SP)	4*	0.94	0.92	0.84	*0.85*
	7	2.16	2.20	2.04	*1.97*
	10	3.49	3.59	3.38	*3.26*
	20	8.30	8.05	7.94	*8.03*
	26	11.56	11.34	11.12	*11.12*

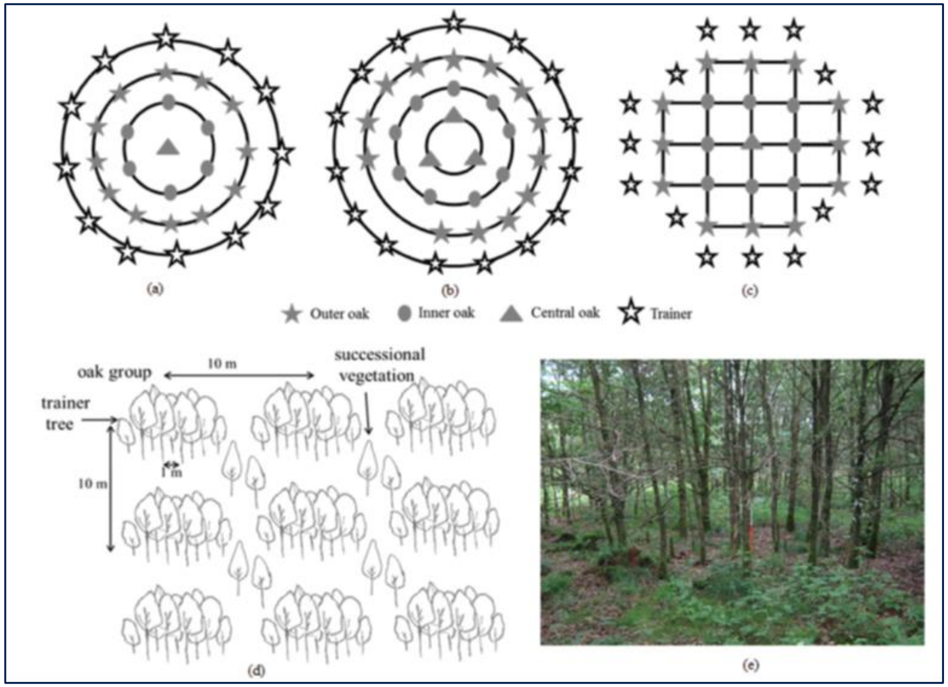
Top heights (m) of four tree species (pure vs mixed stands) at given age (Brown, in: Cannell et al. 1992)

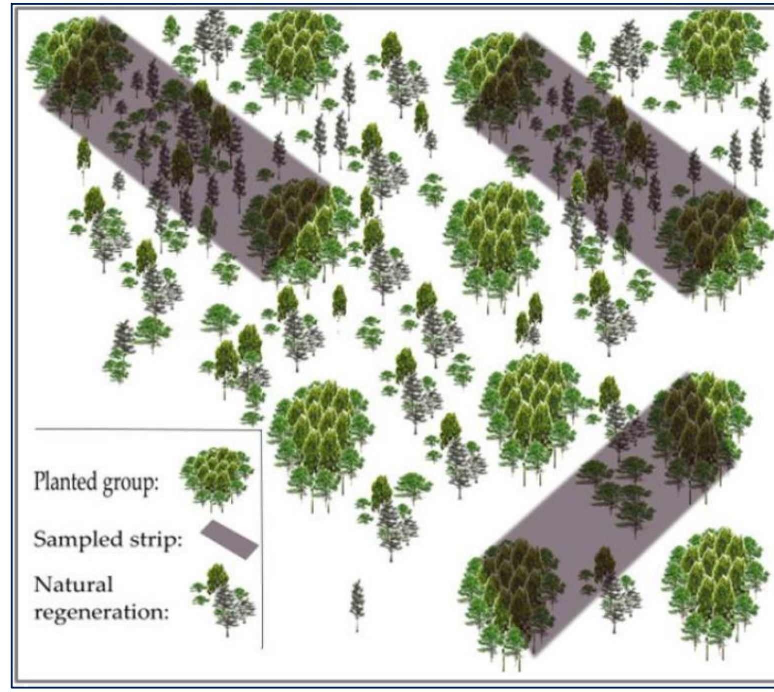
→ **Established silvicultural knowledge and consequential measures**

- the choice and initiation of manageable tree species admixtures

- old strategy created by Mortzfeld (1896)
- groups of 5 plants and distances of 10 m between the groups (Bilke 2004)

→ Established silvicultural knowledge and consequential measures





- group/cluster planting of 10 to 13 oak trees (60 to 100 groups per ha) (Saha et al. 2017)
- 19 to 27 trainer trees (hornbeam, lime trees, beech) surrounding the oak groups

- compared to row plantings: (i) group plantings show better qualities, (ii) five times higher basal area of natural regeneration, (iii) more homogeneous spacing between potential future crop trees (Skiadaresis et al. 2016)

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→ creating admixtures of oak and coniferous tree species in groups or clusters as compromise between ecological and economical targets in practice

→ group/ cluster size depends on interspecific competition pressure (tree species combinations)

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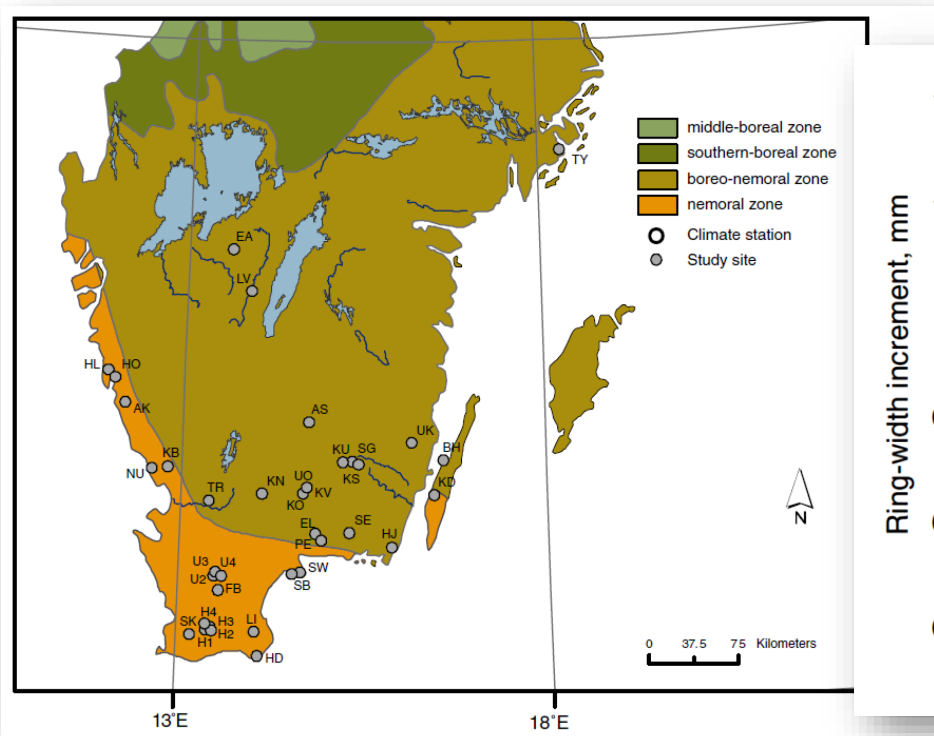
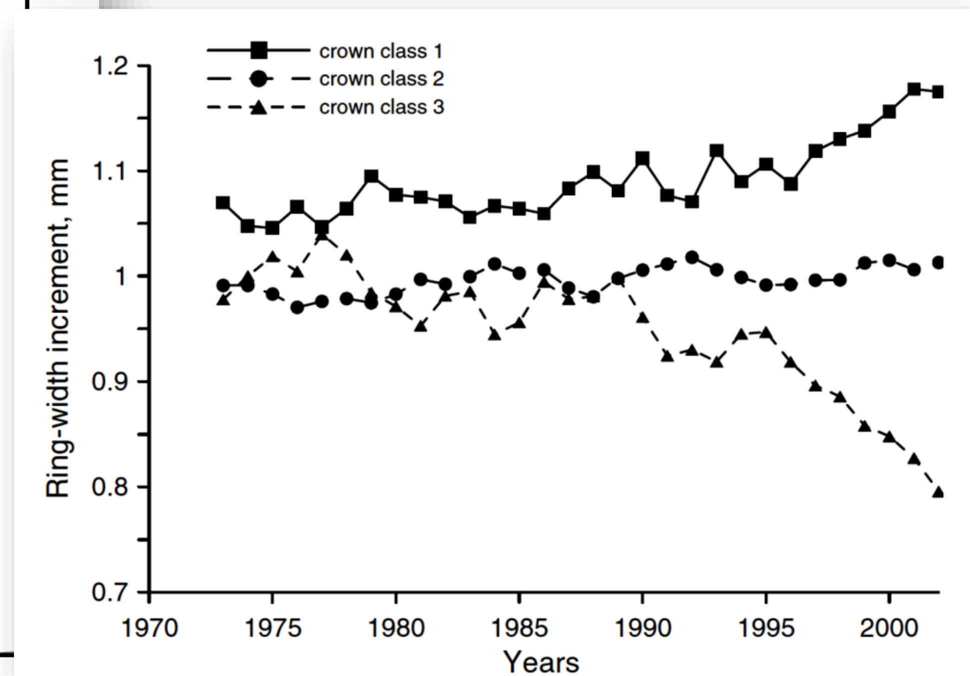
- Crown exposure and position: Seed/ acorn production



Location of study sites and climatic stations (SNA, 2001).

(Drobyshev et al. 2007)



Growth pattern of trees belonging to different classes of crown condition over the period 1973–2002

- **Seed/ acorn production: mast years of Quercus spp.**

"*Mast-seeding is the synchronous production of large seed crops within a population or community of species every two or more years*." (Sork 1993)

"*Mast seeding is the phenomenon of plant populations producing abundant seed quantities, which exceed the average amount of seeds in a flowering year.* "
(Nussbaumer 2016)

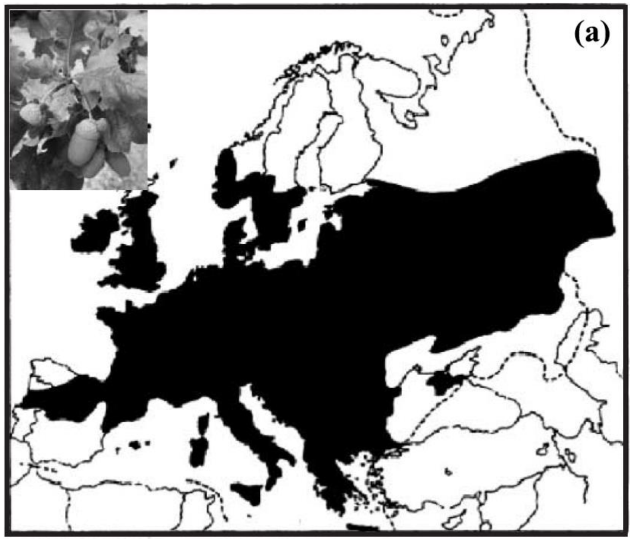
Quercus spp. are classified as "**normal masting**" (Kelly 1994):
- bimodal seed output or with great variation
- seed year resources are diverted from vegetative growth

Characteristics of mast-seeding (Liebhold et al. 2004):
- temporal variability and **relative spatial synchrony (≤ 10 km)**

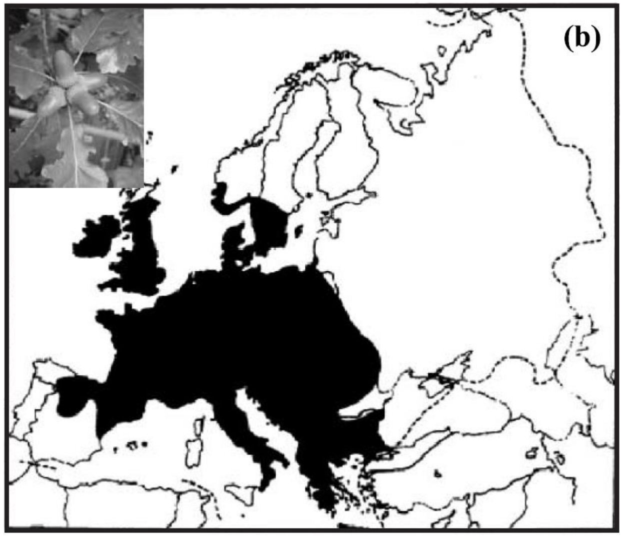
- Genetic constitutions: Pollination and flowering

- monoecious (= male + female flowers are found on the same tree) → wind-pollinated
- male flowers (♂ catkins) appear with leaves (late April to early May)
- female flowers (♀) are very small appear with shoot growth

Pedunculate oak (*Quercus robur*)



Sessile oak (*Quercus petraea*)



Petit et al. 2003

Quality aspects density as a key driver for intraspecific differentiation processes and quality

<u>Natural regeneration</u> established by jays under the shelter of S. pine

- proportion of oaks with good quality between 4 % and 90 % (Stimm & Knoke 2004)

stem form	1 straight	2 + 3 slightly crooked	4 crooked	5 curved
proportion	4.8 %	16.5 %	13.5 %	65.2 %

crown form	1 not forked	2 crown fork	3 stem fork	4 multiple forks
proportion	27.8 %	58.6 %	10.2 %	3.4 %

- different classification systems developed i.a. by Gockel (1994)

Quality of oaks originally established by jays (Stähr & Peters, 2000)

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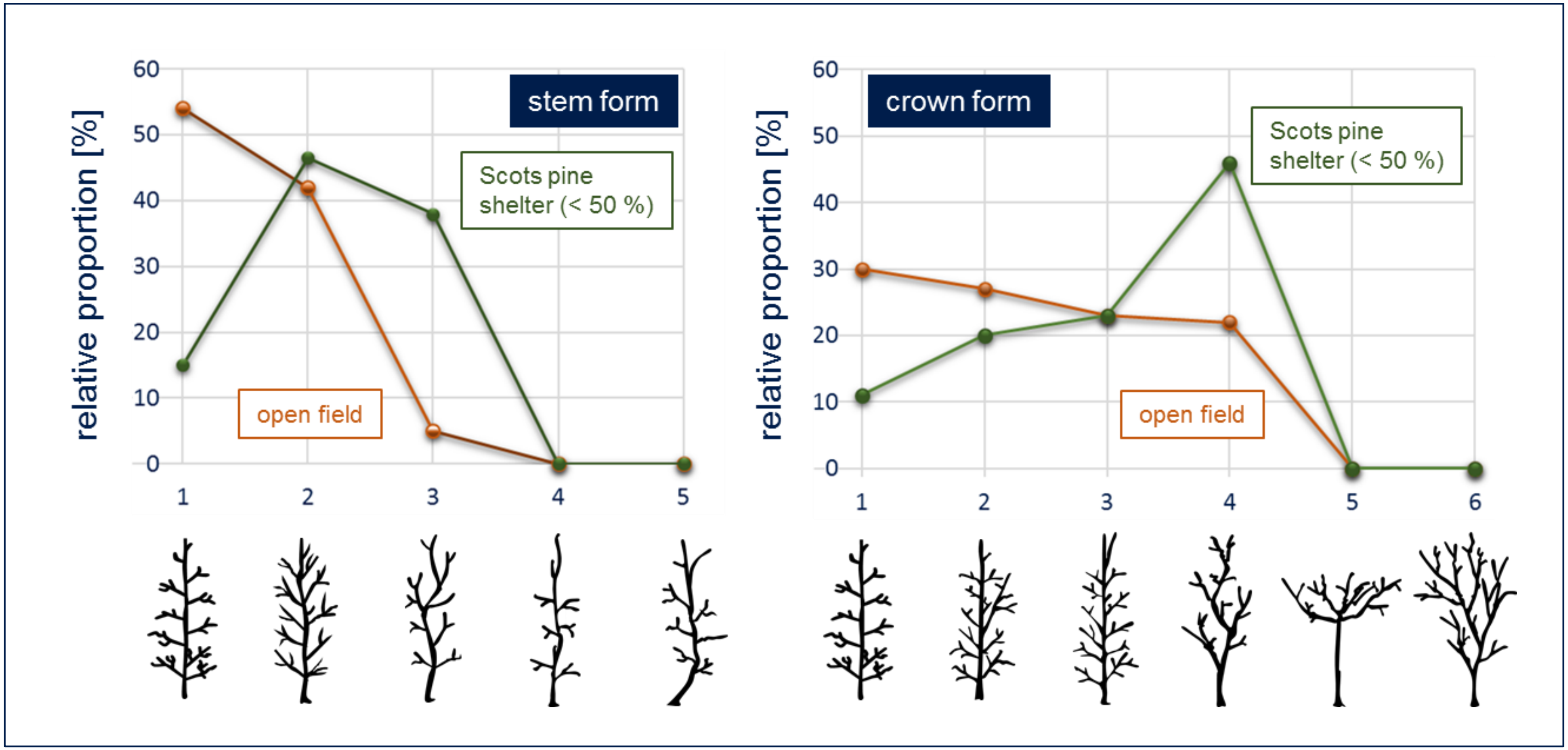
Established juveniles: quality aspects

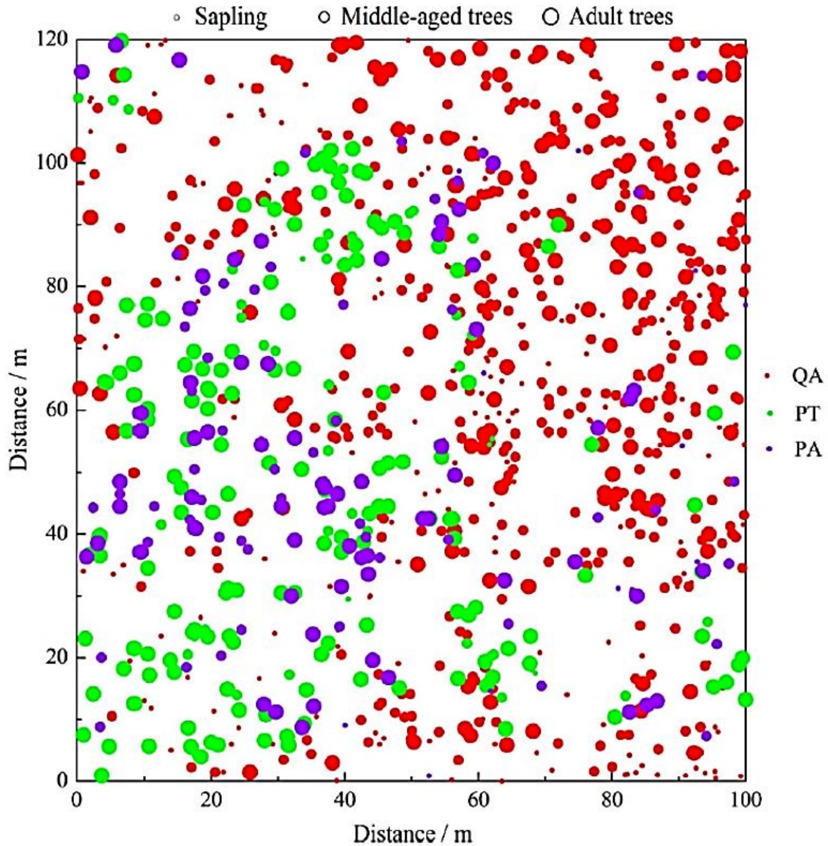
Regeneration established by **advanced plantings**

- long-term **shelter of pine trees** reduces the density of oaks



→ Established silvicultural knowledge and consequential measures

- spatial analyses in pine–oak mosaic mixed forest in the Qinling Mountains, China



Kang et al. (2017), *Quercus aliena*, *Pinus armandii*, P. tabuliformis

- spatial distribution patterns vary with developmental stages
- interspecific associations for saplings of all species were uncorrelated
- negative associations between QA and PT (2 - 27 m) and PA (7 - 22 m)
- positive associations between PT and PA

→ spatial associations and dbh-frequency distributions lead to a continuously replacement of pine species