Penetration of weeds into the herbaceous understorey and soil seed bank of a Turkey oak-sessile oak forest in Hungary

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Abstract: Intensification of land use in the last few decades resulted in an increased rate of fragmentation of natural forest habitats. With decreased patch size but increased total borderline length the influence of the surroundings also increased. The extent of influence is especially crucial where the forest stands are adjacent to agricultural lands. We studied the vegetation (cover) and seed bank (soil samples, seedling emergence) along adjacent stands of an abandoned vineyard and edge and interior of an oak forest community (Quercetum petraeae-cerris) widespread in Central-Europe, using five transects (16 m^2 plots along each transect). We asked the following questions: (i) How do vegetation and seed bank composition differ between the vineyard and forest interior and (ii) which weeds are able to penetrate into the forest herbaceous understorey vegetation and seed banks from the vineyard? In total, 15 phanaerophytes and 147 herbs were detected. Negatively associated with canopy shading, herb cover proved the lowest in the forest inferior. Few weeds and other ruderals recorded in vineyard penetrated into the forest interior. Mean seed density decreased one order of magnitude from the vineyard to the forest interior (from 20,831 to 2,159 seed/m^2). The seed banks of the abandoned vineyard and edge and forest interior were dominated by ruderals, but decreasing proportion of weeds was detected from the vineyard to the forest interior. Characteristic forest herbs possessed at most sparse seed banks. Our results suggest that high canopy cover mitigates the negative impact of surrounding weedy vegetation on the forest herb layer. Therefore, the effect of surroundings is detectable mostly in the seed banks. We can assume that the formation of an increased ruderal herb cover can be foreseen if canopy opens, because the local propagule sources of forest species are missing from vegetation and soil seed banks.

Nomenclature: Simon (2000).

Abbreviations: SBT – Social Behaviour Types; R – ruderals; RC – ruderal competitors; AC – adventive competitors; W – short-lived weeds; DT – disturbance tolerants; G – generalists; C – competitors; S – specialists; NP – natural pioneers; NMDS – Non-metric Multidimensional Scaling; SBD – seed bank density; MC – mean cover.

Introduction

Intensification of land use in last the few decades resulted in an increased rate of fragmentation of natural forest habitats (Laurence and Yensen 1991, Jacquemyn et al. 2001, Eriksson et al. 2002, Devlaeminck et al. 2005). With decreasing patch size, an increase of total borderline length of remained forest stands was typical (Honnay et al. 2002). Thus, the influence of the surroundings on forest vegetation also increased (Jacquemyn et al. 2001, Devlaeminck et al. 2005). The extent of influence is especially crucial where forest stands are adjacent to agricultural lands (Cadenasso and Pickett 2001, Honnay et al. 2002).

Weedy species occur in high abundance in agricultural lands; weeds have effective spatial dispersal ability and/or persistent seeds (Thompson et al. 1997, Honnay et al. 2002). Thus, weed seeds originating from adjacent sources have a high potential to penetrate and incorporate into the forest seed bank. These species remain undetectable in vegetation until some disturbance occurs which makes the environment suitable for their germination (Devlaeminck et al. 2005).

Most of the former studies concentrated on the changes in aboveground vegetation from exterior to forest interior according to a soil moisture, temperature or light transmittance gradient (Williams-Linera 1990, Palik and Murphy 1990, Camargo and Kapos 1995, Oosterhoorn and Kappelle 2000). Only a few studies have paid attention to the influence of surroundings on the seed banks of forests (but see Cadenasso and Pickett 2001, Devlaeminck 2005, Lin and Cao 2009).

We studied the vegetation and seed bank of the herbaceous understorey in weedy abandoned vineyard and edge and adjacent forest interior of an oak forest community (Quercetum petraeae-cerris) widespread in Central-Europe. Our main objective was to evaluate the influence of the vineyard on the forest understorey and seed banks. We asked the following specific questions: (i) How do vegetation and seed bank composition differ between the vineyard and forest interior and (ii) which weeds are able to penetrate into the forest understorey vegetation and seed banks from the vineyard?

Materials and methods

Site description and history

The study site was the Síkfőkút Project nature reserve, located 6 km NE of the town of Eger in the hilly region of Bükk Mountains (ca. 47° 90' N; 20° 46' E, 320-340 m a.s.l.). The climate is moderately continental characterised by a mean annual temperature of 9.9 ^{o}C (summer half-year mean around 17.0 ^{o}C, and the winter half-year around 2.8 ^{o}C). The mean annual precipitation ranges typically from 500 to 600 mm, the highest amount of which falls in the May-July period. The most frequent wind directions are south-west and north. The 64 ha reserve is covered by an even-aged, ca. 100-years-old Turkey oak–sessile oak forest (Quercetum petraeae-cerris), and surrounded by vineyards intensively managed until the 1980's (Jakucs 1985). During the 80's the composition of the tree layer was changed substantially. During a spontaneous oak decay, about one third of the oak trees were perished and the canopy layer was opened. Several trees and shrubs like *Acer campestre, A. tataricum, Crataegus monogyna, Quercus petraea* and *Qu. cerris* rapidly formed a dense second canopy layer (Kotroczó et al. 2008, Krakomperger et al. 2008), which is also typical nowadays. The intensive management of the vineyards was ceased and most of the vine was cut at the end of 1990's, partial irregular cultivation by crop production was terminated and a dense herb vegetation with high cover of weeds and other ruderals was formed.

Sampling setup

We selected five NE situated transects headed from the vineyard to the forest interior in March, 2008. Each transect was 100 m long and consisted of eight 4 m × 4 m plots as shown in Figure 1. Two of the plots were placed in abandoned vineyard vegetation, one plot in the forest edge and five plots in the forest interior. Percentage cover of vascular species was recorded in June, 2008. In the same plots the seed bank was sampled after the snow melt in late March, 2008. In each plot, 6 soil cores were drilled (4 cm diameter, 10 cm depth). Cores drilled from the same plot were pooled to decrease sample heterogeneity. The seed bank was analysed with the seedling emergence method with sample volume reduction by sieving (ter Heerdt et al. 1996, Thompson et al. 1997, Csontos 2001). In a bulk reduction procedure vegeta-

tive organs were retained by washing over a coarse sieve (3.0 mm mesh), while the seed-free fine soil components were removed on a 0.2 mm fine mesh (ter Heerdt et al. 1996). Sample volume was reduced by 65-70%. Concentrated samples were spread in a maximum 3-4-mm-thick layer on trays, previously filled with 4 cm of normal (lower layer) and 4 cm of steam-sterilized potting soil (upper layer). Trays were placed under natural light in a greenhouse shaded with Rachel nets from early May to August. Temperature varied typically between 30 ^{o}C/18 ^{o}C at day/night. Seedlings were regularly counted, identified then removed (Csapody 1968). Unidentified seedlings were transplanted and grown till identified. In early July, when no new seedlings emerged, watering was stopped, dried sample layers were crumbled and turned. In early September watering was re-started and continued until late October. Germination altogether lasted for 37 weeks. Seed rain as contamination was monitored in sample-free control trays filled with sterilized soil only.

Data processing

Seed bank data of three plots of vineyard and edge and five plots of forest interior were pooled, respectively to reach the proper minimum-volume for seed bank analyses (Csontos 2006, 2007). The vegetation data were similarly pooled. A simplified version of Borhidi's SBT (Social Behaviour Types) scale was used during the data processing (Borhidi 1995). According to this, we classified the detected species into ruderal species group (R strategy, sensu Grime 1979) and species group of species characteristic of native habitats (C and S strategy, sensu Grime 1979) including characteristic forest herbs (Borhidi 1995 and 2003). For more detailed analyses within the ruderal species group, we distinguished 'weeds' RC = ruderal competitors + AC = adventive competitors + W = short-lived weeds) and disturbance tolerant species (DT) according to Borhidi (1995). For the detailed classification of species please see Appendix. Student's t-test was used to indicate significant differences in mean species richness and cover scores of abandoned vineyard and edge, and forest interior vegetation and seed banks (Zar 1999). To analyse floristic similarity between vegetation and seed banks NMDS ordination and Sørensen dissimilarity was applied based on presence-absence data (Legendre and Legendre 1998). Statistical analyses were executed using SigmaStat 3.1 and R statistical environment (version 2.11.1, R Development Core Team 2010).
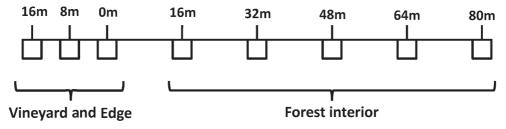

Figure 1. Plot setup of the transects established from abandoned vineyard to oak forest interior. Squares indicate positions of 4 m by 4 m plots.

Table 1. Cover (%) and species richness recorded in vegetation of abandoned vineyard and edge, and forest interior plots (mean±SE). Significant differences were indicated with different superscripted letters (*t*-test, *p*<0.05). The cover scores for the canopy layer were pooled.

Vegetation	Abandoned Vineyard and edge	Forest interior
Species richness		
Phanaerophytes (canopy layer)	2.1±2.0[a]	3.9±0.2[b]
Total herb	21.7±1.0[a]	2.0±0.1[b]
Ruderals	16.5±1.0[a]	1.1±0.2[b]
Weeds (AC, RC, W)	7.3±0.7[a]	0.7±0.2[b]
Disturbance tolerants (DT)	9.2±0.7[a]	0.4±0.1[b]
Competitors and Stress tolerants	5.3±1.0[a]	0.9±0.1[b]
Cover		
Phanaerophytes (canopy layer)	19.5±19.5[a]	95.7±9.3[b]
Total herb	104.5±6.4[a]	6.6±3.3[b]
Ruderals	83.1±6.0[a]	5.9±3.3[b]
Weeds (AC, RC, W)	57.6±8.6[a]	5.4±3.4[b]
Disturbance tolerants (DT)	25.5±4.0[a]	0.4±0.2[b]
Competitors and Stress tolerants	21.4±6.6[a]	0.7±0.1[b]

Table 2. Species richness and seed density (seeds/m^2) recorded in the seed bank of abandoned vineyard and edge, and forest interior plots (mean±SE). Significant differences were indicated with different superscripted letters (*t*-test, *p*<0.05). No seeds of phanaerophytes were detected in the seed banks. Thus, empty lines for phanerophytes were omitted from table.

Seed bank	Abandoned Vineyard and edge	Forest interior
Species richness		
Total herb	15.9±0.6[a]	6.6±0.3[b]
Ruderals	13.8±0.3[a]	4.6±0.4[b]
Weeds (AC, RC, W)	9.0±0.6[a]	2.1±0.2[b]
Disturbance tolerants (DT)	4.8±0.6[a]	2.6±0.2[b]
Competitors and Stress tolerants	2.1±0.3	2.0±0.1
Seed density		
Total herb	20,831±1,833[a]	2,159±202[b]
Ruderals	19,602±1,968[a]	1,708±196[b]
Weeds (AC, RC, W)	16,499±2,094[a]	790±171[b]
Disturbance tolerants (DT)	3,103±774[a]	917±85[b]
Competitors and Stress tolerants	1,229±551	451±18

Results

Vegetation

Altogether 15 phanerophytes were recorded in the vegetation. The most common species were *Quercus petraea*, *Qu. cerris*, *Acer campestre*, and *A. tataricum*. The total cover scores of herbs were high in the abandoned vineyard and edge, whereas in the forest interior only sparse herb vegetation was recorded. The herb vegetation in the vineyard and the edge was characterized by a high cover of weeds and disturbance tolerant species (Electronic Appendix). Species richness and cover of herbs were significantly lower in the forest interior than in the abandoned vineyard and edge (Table 1). In total, 104 herb species were recorded in the vegetation (26 weeds, 35 disturbance tolerants, and 43 competitors and stress tolerants). Out of the detected 25 weed species in the vegetation of the abandoned vineyard and edge two species, *Anthriscus cerefolium* and *Galium aparine* were found in the herb vegetation of forest interior; but only the latter one was detected with a mean cover higher than 5%.

Chelidonium majus was the only weed species found exclusively in the forest interior but with low cover.

Seed bank

Altogether, 81 species emerged from the soil samples (36 weeds, 26 disturbance tolerant and 19 competitor and stress tolerant species, Appendix). The total species richness and that of ruderals were significantly lower in the forest interior than in the abandoned vineyard and edge (*N*=5, *t*=14.2, *p*<0.001, and *N*=5, *t*=19.1, *p*<0.001, respectively; Table 2). The mean total density of seed bank was one order of magnitude lower in the forest interior than in the abandoned vineyard and edge (Table 2, *N*=5, *t*=10.1, *p*<0.001). The density of ruderals was also significantly lower in the forest interior with the same rate as the total density (*N*=5, *t*=9.0, *p*<0.001). The seed bank was dominated by ruderal species everywhere (the proportion of ruderals was 73-98% of total seed bank density, Table 2). Only sporadic seed banks of characteristic forest herbs were detected. The total seed density of weeds was significantly lower in the forest interior than in the abandoned vineyard and edge (*N*=5, *t*=7.5, *p*<0.001). The propor-
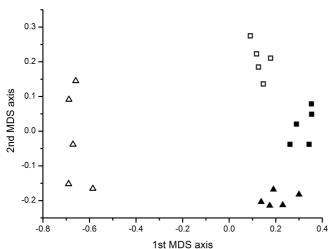
Figure 2. NMDS ordination of the vegetation and seed banks based on the Sørensen dissimilarity of species compositions. Stress = 22.59, Notations: open symbols = vegetation, full symbols = seed bank; triangle = forest interior, rectangle = abandoned vineyard and edge.

tion of weeds within the ruderal group was lower in the forest interior than in the abandoned vineyard and edge. The mean proportion of weeds was 69-93% in vineyard and the edge, and 26-57% in the forest interior.

The seed density of almost all weed species was lower in forest interior than in the abandoned vineyard and edge. Some seed bank weeds like *Chenopodium album, Ch. polyspermum, Conyza canadensis,* and some disturbance tolerants like *Stellaria media* were almost even but low seed densities detected in both sections of the transects (Electronic Appendix). The highest specific seed density scores were detected for the weed, *Stenactis annua*. The seed density of this species decreased about two orders of magnitude from the vineyard and edge to forest interior (from a mean of 12,978 seeds/m^2 to 90 seeds/m^2, Appendix).

Vegetation and seed bank

In total, 147 herb species were detected in vegetation and seed banks. Altogether 38 species were detected both in vegetation and seed banks (12 weeds, 17 disturbance tolerant, and 9 competitors and stress tolerant species; Appendix), 43 species (24, 9, and 10, respectively) were found only in the seed bank and 66 (14, 18 and 34, respectively) were found only in the vegetation. Altogether 61 ruderal species were recorded in the vegetation, out of which 29 species formed also seed bank. The frequent weedy graminoid, *Agropyron repens* detected with high cover in the vegetation of vineyard and edge, did not form a detectable seed bank. None of the detected weeds (3 species) in the vegetation of forest interior had seed banks, and none of the recorded weed species (13) in forest interior seed banks were detected in forest vegetation, but 5 species were present in vegetation of abandoned vineyard and edge (Appendix). Similarity between the seed bank and vegetation proved higher in abandoned vineyard and edge plots. Species composition of the seed bank of forest interior was more similar to seed banks of vineyard and edge than to the vegetation of forest interior (Figure 2).

Discussion

Vegetation and density of seed banks

A lower cover of herb vegetation associated with a higher canopy cover was detected in forest interior compared to abandoned vineyard and edge. The marked differences found between edge and forest interior vegetation correspond with former findings (Brothers and Springarn 1992, Cadenasso et al. 1997, Honnay et al. 2002). The better light availability in the abandoned vineyard and edge can stimulate the germination and establishment of several light demanding species as found also in other studies (Wales 1972, Ranney et al. 1981, Williams-Linera 1990, Aide and Cavelier 1994). We found only sparse herb vegetation in the forest interior. This was most likely caused by the high canopy cover, which prevented the establishment of light demanding species including most of the ruderals (Brothers and Spingarn 1992, Gehlhausen et al. 2000, Honnay et al. 2002). Much lower mean seed density was found in the forest interior than in the abandoned vineyard and edge; the mean seed density was one order of magnitude lower (20,831 vs. 2,159 seeds/m^2). The detected seed densities for the abandoned vineyard fits well the seed density range detected formerly for agricultural lands; but much higher scores were also published (typical scores ranged from about 2,000 to 130,000 seeds/m^2, Cavers and Benoit 1989). For the forest interior, the detected seed density scores were very similar to those found in oak forests (oak-hickory forest USA, 1,181 seeds/m^2; Querceto-Tilietum, Russia, 1,500 seeds/m^2, Pickett and McDonell 1989, Quercetum petraeae-cerris, Hungary, 1,362 seeds/m^2, Csontos 2010a). The detected density scores in forest interior are in the lower part of density range detected for seed banks in temperate forests (published densities range from 66 to 16,700 seeds/m^2, Kjellsson 1992, Csontos et al. 1996a, 1997, Leckie et al. 2000, Devlaeminck et al. 2005).

We found that the similarity between the seed banks of the different parts of transects (abandoned vineyard and edge, and forest interior) was higher than the similarity be-

tween the seed bank and vegetation of the same parts of transects. This phenomenon was also reported by Csontos (2006). It was also found formerly that the species composition of vegetation records was more heterogeneous than that of the seed banks in the same sampling site/plot (Hall and Swaine 1980, Vlahos and Bell 1986). In the present study this was only confirmed for the species composition of the vegetation and seed banks of forest interior (Figure 2), and no such difference was found in abandoned vineyard and edge. This may be caused by several reasons. First, the seed bank along the whole transect was dominated by ruderal species which were mostly missing from vegetation in forest interior but present with high cover in the abandoned vineyard and edge vegetation. Second, several characteristic forest herbs present in the forest interior with at most sparse seed banks, were also found in another study of the authors (Koncz et al. 2010) and by others (Devlaeminck et al. 2005, Csontos 2010b). Finally, the forest understorey was generally characterised by a high spatial patchiness which could be another source of heterogeneity (Benítez-Malvido and Martínez-Ramos 2003).

Weed penetration

Most of the detected ruderal species in abandoned vineyard and edge vegetation did not penetrate into the herbaceous understorey of forest interior. Out of the 48 ruderal species detected in the vegetation of abandoned vineyard and edge, only *Galium aparine* was found with low cover in the forest interior. The rate of invasion of ruderal species into the forest understorey was much lower than in several other studies (Brothers and Spingarn 1992, Cadenasso and Pickett 2001). Many authors have already suggested that presence of ruderals in the herbaceous understorey is restricted by limited light penetration and/or altered soil chemistry (Brothers and Spingarn 1992, Gehlhausen et al. 2000, Honnay et al. 2002). In our case the most likely reason for low establishment of ruderals in the vegetation of forest interior was the high canopy cover, which provides only low levels of light transmittance and suppresses light demanding weeds (Csontos 1996b, 2010b).

The seed banks were dominated by ruderal species (including disturbance tolerants); but a lower proportion of weeds was detected in forest interior than in abandoned vineyard and edge. In spite of a probably high rate of seed production of weed species in abandoned vineyard (Cavers and Benoit 1989), the proven long-term seed persistence (Thompson et al. 1997) and effective spatial dispersal (Andersen 1993) of small seeded weeds, we detected only low density seed banks in forest interior.

This fact may confirm that the forest edges can function as a physical barrier, probably also by decreasing the wind speed, and limiting the arrival of weed seeds into the forest interior, as it was found in other studies (Didham and Lawton 1999, Cadenasso and Picket 2001, Honnay et al. 2002, Devlaeminck et al. 2005). Seeds of several light demanding weed species with known ability to form persistent seed bank

were detected (e.g., *Chenopodium album*, *Ch. polyspermum*) in every part of the transects. Their presence in the soil in addition to former spatial dispersal from abandoned vineyard and edge may also reflect to former successional stages of understorey, where the canopy cover was less dense (i.e., longevity of seeds of *Chenopodium* species can exceed several decades, Harper 1977, Cook 1980, Priestly 1986).

Our results suggest that the high canopy cover can mitigate the negative impact of surrounding ruderal vegetation on the forest herb layer. This negative impact in form of low density but ruderal-dominated seed banks is considerable, because typical species of undisturbed habitats, e.g., long lived seeds of characteristic forest herbs are mostly missing (e.g., Warr et al. 1994, Mitlacher et al. 2002, Koncz et al. 2010). Similar results were found in other studies (Halpern et al. 1999, Bossuyt and Hermy 2001, Bossuyt et al. 2002, Bossuyt and Honnay 2008). In our study, the effect of the surroundings was mostly detectable in the seed banks. This also confirms that soil seed banks provide early signals of weed infestation and invasion before the weeds appear in aboveground vegetation in forest interiors. Thus the analysis of soil seed banks could be the key element of detection which was also suggested by Lin and Cao (2009). Former studies showed that an increased disturbance can promote invasion in forest interior (Laurence 1991). We can assume that the formation of an increased ruderal herb cover can be foreseen if canopy opens, because the local propagule sources of forest species are missing from vegetation and soil seed banks.

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Appendix

Mean cover, seed bank density and frequency scores of herbs detected in the vegetation and/or seed bank. The file may be downloaded from the web site of the publisher at www.akademiai.com.

Appendix. Mean cover (MC, %), seed bank density (SBD, seeds/m^2) and frequency scores (F) of herbs detected in the vegetation and/or seed bank. Notations: **SBT** = Social Behaviour Types according to Borhidi (1995). **Ruderals (R)**: RC = ruderal competitor, AC = adventive competitor, W = short-lived weeds, DT = disturbance tolerants. The first three categories (RC, AC and W) were considered as weeds. **Competitors and Stress tolerants (C and S)**: G = generalists, C = competitors, S = specialists, NP = natural pioneers.

Weeds (AC, RC, W)		Vineyard and edge				Forest interior			
Species	SBT	F	MC	F	SBD	F	MC	F	SBD
Agropyron repens	RC	14	46.8						
Amaranthus retroflexus	RC			8	142			1	5
Ambrosia elatior	AC	1	<0.1						
Anagallis arvensis	W			2	36				
Anthriscus cerefolium	W	1	<0.1			1	<0.1		
Arctium lappa	W	1	0.1						
Artemisia vulgaris	W	7	0.3	10	354				
Ballota nigra	W			5	27			1	5
Bromus sterilis	RC	2	0.1						
Calamagrostis epigeios	RC	1	<0.1						
Capsella bursa pastoris	W			10	372				
Chelidonium majus	W					1	<0.1		
Chenopodium album	RC	1	<0.1	12	195			5	96
Chenopodium hybridum	W							3	16
Chenopodium polyspermum	RC			6	540			7	425
Chrysanthemum vulgare	W	6	1.4	5	168				
Cichorium intybus	W	9	0.8	2	18				
Cirsium arvense	RC	8	0.7	2	18			4	22
Cirsium vulgare	W	1	0.1	2	27				
Conium maculatum	RC			1	18				
Convolvulus arvensis	RC	6	0.2						
Conyza canadensis	AC	1	<0.1	3	45			8	43
Digitaria sanguinalis	AC			2	18			3	16
Dipsacus laciniatus	W	4	<0.1						
Echinochloa crus-galli	AC			3	36				
Galium aparine	W	4	0.2			14	5.4		
Hibiscus trionum	W			2	18				
Lactuca serriola	W			1	9				
Lamium amplexicaule	W			3	18				
Lathyrus tuberosus	W	7	0.6						
Linaria vulgaris	W	5	0.3					1	5
Marrubium peregrinum	W			2	18				
Matricaria inodora	W	4	0.1	4	80				
Melandrium album	W			2	18			3	16
Melilotus officinalis	W	3	<0.1	2	18				
Oenothera biennis	W			2	407				
Plantago major	W			4	36				
Polygonum aviculare	RC			4	115				
Portulaca oleracea	W			4	54			2	22
Rumex crispus	W	2	<0.1						
Setaria glauca	W							1	5
Solidago canadensis	AC	1	0.1						
Sonchus oleraceus	W	1	<0.1						
Stachys annua	W			4	62				
Stenactis annua	AC	12	4.3	15	12,978			12	90
Taraxacum officinale	RC	3	<0.1	3	54				
Thlaspi arvense	W			3	319				
Veronica opaca	W			1	18				
Veronica persica	A			2	18				
Veronica polita	W			6	151				

Disturbance tolerants (DT)		Vineyard and edge				Forest interior			
Species	SBT	F	MC	F	SBD	F	MC	F	SBD
Achillea millefolium	DT	5	<0.1						
Alliaria petiolata	DT					2	<0.1		
Anthriscus sylvestris	DT	1	<0.1						
Arrhenatherum elatius	DT	4	2.6						
Carex muricata	DT							2	12
Carlina biebersteinii	DT	3	<0.1						
Centaurea pannonica	DT	13	2.0	4	45			1	12
Cerastium fontanum	DT	1	<0.1						
Chaerophyllum temulum	DT	1	<0.1						
Chamaenerion angustifolium	DT							3	16
Dactylis glomerata	DT	13	7.4	2	27			1	5
Daucus carota	DT	11	0.2	9	203				
Fallopia dumetorum	DT					3	<0.1	4	22
Geranium robertianum	DT	3	<0.1			4	0.2		
Geum urbanum	DT	10	0.2			2	0.1	1	5
Hieracium umbellatum	DT	1	<0.1						
Hypericum perforatum	DT	6	0.1	10	1646			17	515
Inula conyza	DT	4	1.3						
Juncus articulatus	DT							1	5
Juncus bufonius	DT							1	5
Juncus effusus	DT							1	5
Lepidium campestre	DT	2	<0.1	1	9				
Lolium perenne	DT	2	0.2						
Medicago lupulina	DT	6	0.4					1	11
Moehringia trinervia	DT					2	<0.1	1	5
Origanum vulgare	DT	11	0.6	2	18				
Pastinaca sativa	DT	1	0.1						
Persicaria lapathifolia	DT			2	18				
Picris hieracioides	DT	9	1.4	3	36				
Plantago media	DT	1	<0.1	8	45				
Poa angustifolia	DT			2	18			1	5
Poa compressa	DT	2	<0.1	3	36				
Prunella vulgaris	DT	3	<0.1	4	54			3	27
Ranunculus sardous	DT							1	5
Rumex acetosa	DT			5	58				
Senecio jacobea	DT	3	1.5						
Stellaria media	DT	2	<0.1	7	195			10	112
Tragopogon orientale	DT	2	<0.1						
Trifolium arvense	DT	1	<0.1						
Trifolium repens	DT	3	1.1						
Urtica dioica	DT	4	4.3	7	434			3	27
Veronica chamaedrys	DT	8	5.3	3	36			11	90
Vicia hirsuta	DT	2	0.1						
Vicia tetrasperma	DT	1	<0.1						

Competitors and Stress tolerants (C, G, NP, S)		Vineyard and edge				Forest interior			
Species	SBT	F	MC	F	SBD	F	MC	F	SBD
Agrostis alba	C			2	18				
Ajuga genevensis	G	1	<0.1					2	11
Astragallus glycyphyllos	G	1	<0.1						
Brachypodium sylvaticum	G					1	<0.1		
Bromus inermis	C	1	1.7						
Bromus ramosus	G					1	<0.1		
Buglossoides purpureo-coerulea	S					1	0.1		
Carex digitata	G							1	5
Carex montana	S							2	11
Centaurium erythrea	G	4	0.8	9	814			1	5
Chrysanthemum corymbosum	G	1	<0.1						
Clinopodium vulgare	G	8	0.4						
Convallaria majalis	G					1	<0.1		
Dactylis polygama	G							4	43
Dianthus armeria	G	2	<0.1						
Epilobium parviflorum	G	2	<0.1						
Epilobium tetragonum	G	1	<0.1	7	124				
Festuca pratensis	C	8	2.8						
Filago arvensis	NP			1	9				
Fragaria viridis	G	8	0.6	3	142			1	11
Galeopsis pubescens	G					3	0.2		
Galium schultesii	G							1	5
Hieracium bauhini	G	2	0.3						
Hieracium sabaudum	G	1	<0.1						
Hypericum montanum	G	1	<0.1						
Inula helenium	S	3	0.3						
Inula salicina	G	2	<0.1						
Lactuca quercina	G							1	5
Lathyrus niger	G	1	<0.1						
Lathyrus vernus	G					2	<0.1		
Melampyrum nemorosum	G	3	<0.1						
Melandrium viscosum	S	1	<0.1						
Melica uniflora	C					4	<0.1		
Poa nemoralis	C	1	<0.1	2	18	1	<0.1	9	59
Poa pratensis	G	9	4.9						
Polygonatum latifolium	G					1	<0.1		
Pulmonaria mollissima	G	1	<0.1						
Ranunculus polyanthemos	G	4	<0.1						
Solidago virga-aurea	G	4	0.4					1	5
Stachys sylvatica	G					1	<0.1		
Symphytum nodosum	G					2	<0.1		
Teucrium chamaedrys	G	1	<0.1					1	5
Thalictrum lucidum	G	1	<0.1						
Turritis glabra	G							3	21
Typha cf. angustifolia	C			5	88			20	244
Verbascum chaixii	G			1	9				
Verbascum lychnitis	G	4	<0.1						
Veronica officinalis	G	1	<0.1					2	11
Vicia lathyroides	NP	3	<0.1					1	5
Vinca minor	C					1	<0.1		
Viola hirta	G	2	<0.1			1	<0.1		
Viola sylvestris	G					1	<0.1		
Viscaria vulgaris	S	1	<0.1						