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INTRASPECIFIC PHENOTYPIC VARIABILITY OF THE HERBACEOUS SPECIES *DAUCUS CAROTA* (APIACEAE) USED FOR RESTORATION PURPOSES

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For restoration purposes nature conservation preferably requests the use of local seed sources based on the "local-is-best" (LIB) approach. However, counter-arguments against this usage are potential benefits by increased variation, which could be beneficial especially in times of global change. We here investigate intraspecific morphological variability of one of the most common herbaceous, insect pollinated and zoochorous plants from seed mixtures used for landscape restoration processes in central Europe, the wild carrot, *Daucus carota* L. (Apiaceae). Our results show that *D. carota* features no vegetative but two generative characters that significantly differed among plants originating from seeds of natural (I) and restored (R) sites. We could show that effects of mowing always overlay origin-specific characteristics. The earlier genetic analysis did not support a regional provenance concept for restoration purposes, while slight differences in phenological parameters related to fitness pinpoint to 'mix and match-admixture provenancing' as a compromise strategy.

Key words: *Daucus carota*, local-is-best approach, non-local genotypes, restoration, vegetative and generative fitness parameter

INTRODUCTION

An ever changing landscape due to building activities evokes the management of restoration processes. Particularly frequent restoration projects in Germany are the greening of edges after road construction. For these projects the use of mostly undefined or non-local seed sources of herbaceous species was and is common practice. Reasons for the common practice of using non local seed provenances are significantly lower prices compared to local provenances and easy availability of large amounts of non-local seed compared to regional seed (Burton and Burton 2002, Kettenring *et al.* 2014). However, from 2020 onwards seed from regional provenances has to be used as part of the nature protection and landscape conservation act (BNatSchG §40-1, 2010) to preserve the local genotypic diversity, hence, the local allelic richness (Hughes *et al.* 2008). This local-is-best approach (LIB) is justified to preserve the genetic legacy resulting from a history of natural selection in local environments (Johnson *et al.* 2010, Jones 2013, Montalvo *et al.* 1997, Sackville Hamilton 2001). From a genetic point of view there are four major arguments for the LIB approach: (1) Interbreeding between non-local and local provenances can lead to the homogenisation of the genetic structure of populations (Hughes *et al.* 2008). (2) Genetic swamping can alter the genetic memory for this location, especially the genetic legacy resulting from a history of natural selection (Montalvo *et al.* 1997). (3) Maladaptation resulting from artificial selection and the new introduced provenances could rather poorly perform in the new environmental conditions (Bischoff *et al.* 2010, Hufford and Mazer 2003). (4) Outbreeding depression as a result from crossings among genetic distinct populations from different environments featuring reduced fitness (McKay *et al.* 2001). Adherence to the LIB theory resulted mostly in studies concerning better fitness and performance of the local plant material, as summarised by Jones (2013). Thus, the four main arguments of the LIB approach mostly correlate with morphological differences. The research of restoration ecology has increased significantly in the recent years and the focus of many studies is mostly the choice of the seed sources (Bell and Hobbs 2007, Breed *et al.* 2018, Bucharova 2017, Bucharova *et al.* 2017, 2019, Durka *et al.* 2017, Harris *et al.* 2006, McKay *et al.* 2001, Stingemore and Krauss 2013). This recently led to the establishment of seed transfer zones and regions for grassland species in Germany (ErMiV 2011, Schröder and Prasse 2013). These seed transfer zones are defined based on geology, biogeography, climate, and other biophysical criteria. The basic assumption here is that the criteria for delineation also influence the spatial genetic structure of plant species subject to the condition that the patterns of genetic differentiation between species are largely similar (Durka *et al.* 2017).

We here investigate intraspecific morphological variability of one of the most common herbaceous, insect pollinated and zoochorous plants from seed mixtures used for landscape restoration processes, the wild carrot, *Daucus carota* L. (Apiaceae). Seeds were collected from populations that were formerly restored with non-local seed material (in the following R = restored) and from nature conservation areas or from natural sites which have not been modified or re-sown during the last 60 years (in the following I = indigenous; Posselt 2000). In a common garden approach we analysed the morphological variation between samples from I and R sites. Since plants in natural habitats, even in nature reserves, are subject either to grazing or mowing at least once a year, a part of the grown individuals per study site was cut to simulate the natural conditions of grassland habitats.

We hypothesise, that individuals from I and R populations differ in their vegetative and generative morphology and that variation is stronger, if grazing or mowing is simulated. The results will show whether strict adherence to the local-is-best approach for *D. carota* can be recommended, hence non-local seed usage should be omitted.

MATERIAL AND METHODS

Plant species

Daucus carota is a biennial species with bristly hairy stems that reach heights up to 50 to 120 cm (Berger *et al.* 1975). *D. carota* forms a rosette in its first year and flowers usually in the second year from June to September (Düll and Kutzelnigg 1992). The inflorescence is a flat and dense umbel with small white flowers. Mostly a black-purple flower can be found in the centre of the umbel. This so-called sham bloom will probably mimic a fly and thus might serve as an "invitation" to other flies for a visit. Outcrossing is enforced by a pre-male flowering stage (protandry). *D. carota* is obligate cross-pollinated with limited adaptations to species-specific pollinators (Berger *et al.* 1975). Pollinators are flies, bees or beetles (Düll and Kutzelnigg 1992). Especially *Andrena* spp. are frequent visitors to the flowers of wild carrot (Düll and Kutzelnigg 1992). Some of these pollinators fly distances up to 2 km (Düll and Kutzelnigg 1992). Additionally bees are among the pollinators and this species group can travel up to 10 km. The seeds are adapted to epizoochoric dispersal of mammals by featuring bristly hairs that protrude from the ribbed seed surface (Berger *et al.* 1975, Rong *et al.* 2010).

Typical habitats of *D. carota* in Germany are meadows, thickets, and areas along railroads and roadsides with some kind of disturbance, while the species is also common in extensively managed grasslands (Düll and Kutzelnigg 1992). The species' native distribution covers large parts of Europe, eastern and central Asia, and the Mediterranean region (Berger *et al.* 1975). According to Berger *et al.* (1975) ten subspecies of *D. carota* are recognised throughout the species' whole distribution range. In Germany, so far only *D. carota* subsp. *carota*, next to the garden cultivar *D. carota* subsp. *sativa*, has been reported (Düll and Kutzelnigg 1992). Since subsp. *carota* is widespread throughout Europe, North Africa, eastern and central Asia, the taxonomic affiliation does not provide any indication of the origin of the seeds of the restored sites.

Plant sampling

In autumn 2011 seeds of *D. carota* were sampled from 17 different populations and approximately 20 individuals per population in central Germany (Fig. 1). The distance between sampled individuals within populations was at least two meters to optimise the coverage of site specific population diversity. Nine of the populations were indigenous (I), and eight were restored populations (R). The populations were not randomly spaced across the landscape. Road authorities provided information about the year of restoration for the R sites (Table 1) as well as the percentage of *D. carota* (0.1%) seeds in the applied

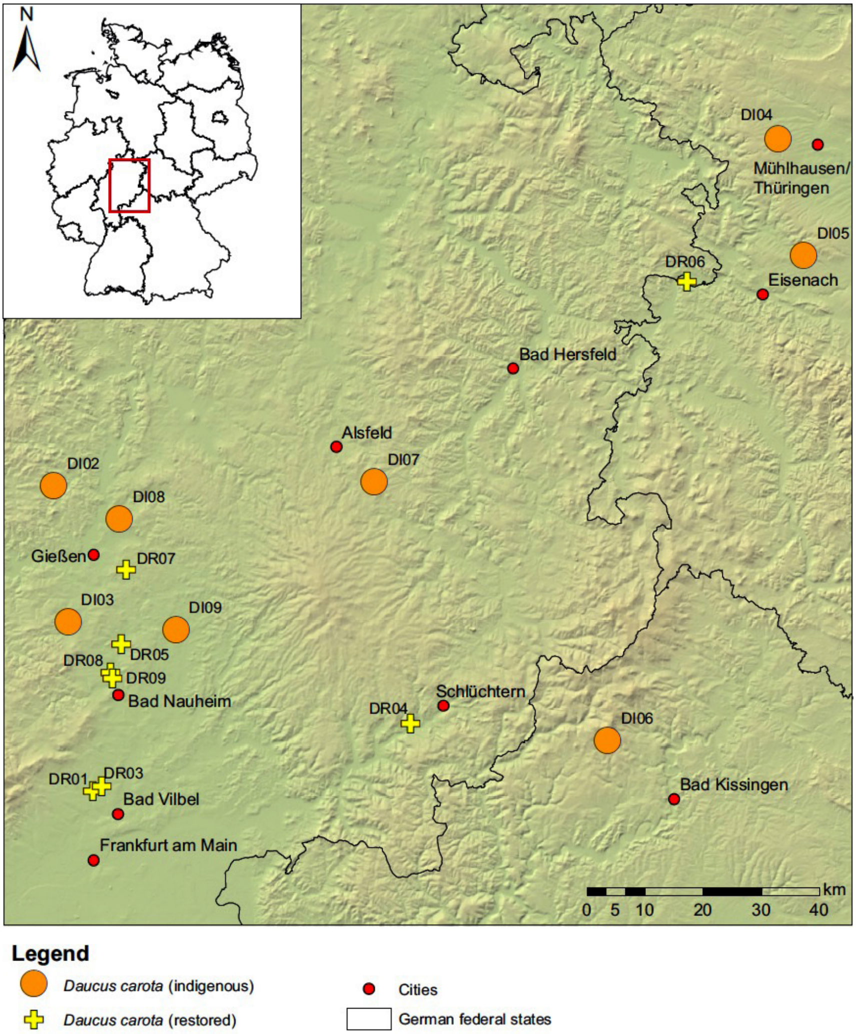

Fig. 1. Map of sampled *Daucus carota* populations in the investigation area in central Germany (Hesse, Thuringia and Bavaria). The red box in the top-left map shows the area in Germany. Indigenous sites (I) of the species are depicted in the map as orange circles and the restored sites (R) are pictured as yellow crosses. Labels correspond to those in Table 1. Map was prepared with ArcGIS Desktop (ArcGIS Desktop 10.2.2., ESRI)

Table 1

Surveyed *Daucus carota* populations. Abbreviations: ID = identification Number, DI = indigenous populations, DR = restored populations, location in accordance to the nearest village or town, normal = number of non-mowed individuals and cut = number of mowed individuals, both of them (normal and cut) are for the elevation of generative fitness, vegetative = examined parameters of vegetative fitness, coordinates north (N) and east (E), management = Type of maintenance *Daucus carota*, Management/yr = Management / year of restoration

ID	Location	Normal	Cut	Vegetative	N	E	Management/yr
DI01	Pfungstadt	19	18	18	49° 50′ 02.0″	8° 34′ 56.5″	extensive
DI02	Kirchvers	20	10	17	50° 41′ 26.4″	8° 34′ 45.1″	extensive
DI03	Niederkleen	20	19	19	50° 28′ 50.8″	8° 36′ 59.2″	sheep
DI04	Eichsfeld	17	17	17	51° 13′ 14.6″	10° 21′ 30.1″	sheep
DI05	Berka v. d. H.	17	17	19	51° 02′ 22.5″	10° 24′57.2″	sheep
DI06	Schwarzer Berg	18	17	18	50° 17′ 34.5″	9° 55′ 13.7″	extensive
DI07	Lauterbach	19	19	19	50° 41′ 46.6″	9° 21′ 34.8″	sheep
DI08	Daubringen	13	13	15	50° 38′ 24.9″	8° 44′ 20.6″	intensive
DI09	Hungen	17	16	18	50° 28′ 03.7″	8° 52′ 39.6″	sheep
DR01	Erlenbach 1a	20	20	20	50° 13′ 08.5″	8° 40′ 45.6″	2004
DR03	Erlenbach 2a	15	14	17	50° 13′ 34.6″	8° 42′ 05.5″	2004
DR04	Steinau	14	14	14	50° 19′ 24.1″	9° 26′ 45.6″	1994
DR05	Griedel	20	20	20	50° 26′ 50.3″	8° 44′ 42.9″	1996
DR06	Herleshausen	20	19	20	51° 00′ 08.1″	10° 07′ 49.5″	2003
DR07	Fernwald	16	16	20	50° 33′ 40.7″	8° 45′ 27.9″	2003
DR08	Bad Nauheim	20	19	20	50° 24′ 09.7″	8° 43′ 15.1″	1996
DR09	Bad Nauheim	20	20	20	50° 23′ 33.0″	8° 43′ 32.4″	1996
Total I		*160*	*146*	*160*			
Total R		*145*	*142*	*151*			
Total		*305*	*288*	*311*			

seed-mixtures. Although no information about the origin of the seed material was available, local seed providers as source of the seeds can be excluded. We cannot guarantee that the individuals from restored sites are identical to those introduced 10–20 years ago as gene flow from wild but also cultivated carrot all over the country from gardens cannot be excluded (Mandel *et al.* 2016, Shim and Jørgensen 2000). Furthermore, admixture of pollen and propagules between sites cannot be omitted. Therefore we do not know, where the seeds originated from, and under which climatic and ecological conditions the seed material has been produced.

Table 2

Effects of mowing (k = 2, mowing or not), origin (k = 2, indigenous or restored populations), the interaction of mowing and origin (M x O) on *Daucus carota*. Abbreviation: df = degrees of freedom, MQ = sum of mean squares, F = variance ratio, *p* = error probability, significant *p*-values < 0.05 are written in bold. Traits are indicated by numbers in parentheses

	date of highest amount of umbels (10)				no. of flowering umbels (12)				no. of fruiting umbels (14)			
	df	MQ	F	*p*	df	MQ	F	*p*	df	MQ	F	*p*
Intercept	1	**1010676000000.0**	**1634439000.0**	**< 0.001**	1	**33505.3**	**1417.5**	**< 0.001**	1	**20375.9**	**1240.1**	**< 0.001**
Mowing (M)	1	**15176.9**	**24.5**	**< 0.001**	1	**672.9**	**28.5**	**< 0.001**	1	**419.6**	**25.5**	**< 0.001**
Origin (O)	1	**6823.7**	**11.0**	**< 0.001**	1	**103.0**	**4.4**	**0.037**	1	23.5	1.4	0.231793
M x O	1	851.5	1.4	0.241	1	79.6	3.4	0.067	1	38.7	2.4	0.125661
Error	607	618.4			607	23.6			593	16.4		

Indigenous sites were selected with support of the "Association of German wild plants and seeds producers e. V.". To minimise biases or crossbreeding with a different intraspecific genotype, a distance of at least nine kilometre to adjacent populations with non-local seed sources was kept (Posselt 2000, Schröder and Prasse 2013).

Common garden approach

Of each individual of each study site 60 seeds were sown in spring 2012. Germinated seedlings were cultivated in single pots with uniform nutrient-poor soil and regular watering and weeding. The common garden experiment allowed for taxonomic verification. We could not detect other than *D. carota* subsp. *carota* among our samples.

The randomly selected seedlings of each population were arranged without grouping. One third per study site grew up without treatment and another third was cut to 15 cm on 31.07.2013 to simulate grazing or mowing as natural conditions of grassland habitat. All main shoots were cut, no matter if they were already in flower or not. The last third was harvested on 20.06.2013 to count and measure the vegetative morphological variation. The data collection took place in 2013 in and throughout the growing season.

We tested two models of influence on morphological variation: (1) the effect of origin (I, R) for 311 individuals (vegetative characters only, Table S1), and (2) treatment (mowed, not-mowed) and origin (I, R) for 305 and 288 individuals respectively (generative characters only, Fig. 2, Table 2 and Table S2).

Examined parameters of vegetative morphological variation were (1) number and (2) size of the leaves, (3) length and (4) diameter of the root, and the weight of the leaves as (5) fresh and (6) dry matter, and of the root (7 and 8), respectively. They were quantified once, when one third of the plants were harvested.

The parameters of generative morphological variation were measured two times per week. They were: (9) day of first flowering, (10) day of maximum number of flowering umbels, (11) day of maximum number of fruiting umbels (12) number of flowering umbels, (13) number of fruiting umbels, (14) number of umbels with ripe fruits only and (15) the weight of ripe umbels, (16) day of death (after seed set, the plants turn brown and die off). Additionally the following derivatives of the former generative parameters were calculated: (17) duration from first flowering to highest amount of fruiting umbels, (18) number of simultaneously flowering and fruiting umbels, (19) and the date of this, (20) duration from first flowering to the first ripe umbel and (21) duration from first flowering to the end of the growing season.

Data analysis

All statistical analyses were carried out using the program STATISTICA (v. 10.0, Statsoft Inc., Tulsa, Oklahoma, USA) by using the raw data. Effects of the single factors *origin* (k = 2, restored vs. indigenous) and *mowing* (k = 2, mowed vs. not mowed) and the factor combinations were assessed with a multi-factorial analysis of variance (ANOVA). Subsequently, significance of differences between treatments was assessed with a Tukey Test (Table 2 and Fig. 2 a-c).

RESULTS

In total 904 individuals were examined with the ANOVA (Table 1). 311 individuals were examined only for vegetative characters (traits 1–8), 160 individuals from I and 151 from R sites (Table S1). All of the analysed vegetative characters showed no significant differences between sites. 305 individuals were not mowed and 288 were cut to simulate mowing. The first group consisted of 160 indigenous and 145 restored individuals and the second group of 146 indigenous and 142 restored individuals, respectively.

Only two of the 13 analysed generative fitness parameters (traits 9–21) featured significant effects between R and I populations (significant traits in Table 2 and Fig. 2 and some exemplary non-significant traits in supplements Table S2). Comparing the total number of flowers per individuals and the date of this (trait 10 and 12) we see in the dataset that the indigenous plants

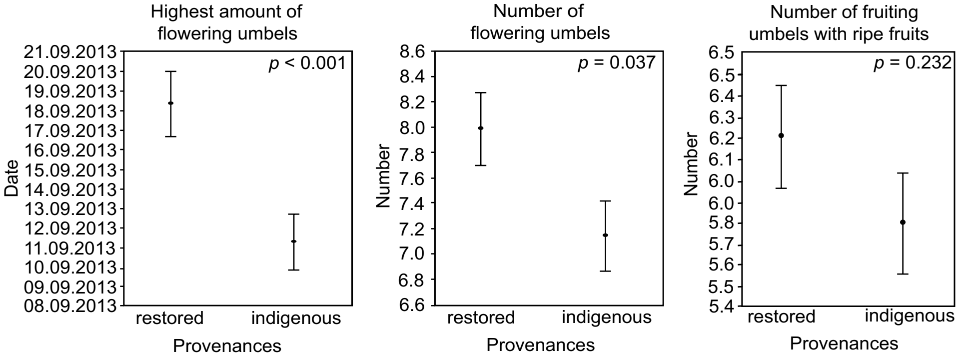

Fig. 2. ANOVA of three generative fitness parameters of *Daucus carota*: (a) comparative date of the highest amount of flowering umbels (trait 10, significant), (b) number of flowering umbels (trait 12, significant), (c) number of fruiting umbels with ripe fruits (trait 14, not significant). The points show the mean of the various fitness parameters of the different provenances (restored and indigenous) and the ± standard deviation; *p*-values for comparisons between restored and indigenous provenances are from a Tukey HSD test using the residuals of the ANOVA for the factor origin

had the maximum number of flowering umbels earlier in the summer than the restored provenances (Table 2 and Fig. 2a); the indigenous provenances had reached their highest amount on 11.09.2013. The restored provenances, however, had their highest amount of flowering umbels one week later on 18.09.2013. At the same time the indigenous plants also had fewer flowering umbels (on average 7.2 per individual, trait 12) than the restored provenances (on average 8 per individual, Table 2, Fig. 2b). Nevertheless, at the end of the growing season both provenances had surprisingly similar numbers of mature umbels (trait 14) and the overall difference of the provenances were not significant (Table 2 and Fig. 2c).

ANOVA showed that cutting always had a significant influence on all analysed generative fitness parameters, regardless of the origin of the samples. Thus, effects of mowing always mask origin-specific characteristics, which than disappear.

DISCUSSION

Despite knowing that semi-natural, extensively used species rich grassland in Europe is threatened by land-use intensification, climate change and habitat destruction (Reid 2005), only few studies investigating fitness parameters of common and widely distributed herbaceous plants exist (Dolan *et al.* 2008, Miller *et al.* 2011, Ritchie and Krauss 2012). Fitness analyses of arable weeds and meadow species are rare, although it is assumed that plants of local genotypes and origin generally have better fitness (Jones 2013, Kawecki and Ebert 2004, Keller and Kollmann 1999, Leimu and Fischer 2008, Linhart and Grant 1996). In most grassland restoration studies the identity of the seed sources is an important issue (Durka *et al.* 2017).

In our analysis, in the herbaceous meadow species *D. carota,* only three of all tested generative and vegetative fitness parameters differed between individuals of R and I sites. Our result supports earlier findings by Bucharova *et al.* (2017), who analysed biomass differences in a reciprocal transplant experiment of *D. carota* at four different sites in Germany and also discovered mostly insignificant vegetative fitness differences. However, our data support the hypothesis that fitness-related traits are generally less differentiated than phenological traits (Durka *et al.* 2017). The phenological differences between individuals at I and R sites in our analysis indicate genotypic integrity. It is well known that flowering time is often strongly differentiated along geographical gradients, even within perennial plants (e.g. Kawakami *et al.* 2011, Montague *et al.* 2008) and differences in phenology-related traits likely reflect plant adaptation to different latitudes, climate and seasonality, or different plant strategies in different environments (Durka *et al.* 2017). Although we could not guarantee that the genotypes from restored sites are identical to those introduced 10–20 years ago, we detected phenological differences, which potentially are indicative for non-local adaptation processes.

An earlier flowering of a common herbaceous species (trait 10) may influence the activity of pollinators and therefore influences the competition between flowering plants. Moreover early flowering plants support ecosystem services in form of nutrition for flower visiting insects. This was confirmed in previous studies by Ladizinsky (1985) and Ellstrand and Elam (1993) and is supported here. At the end of the growing season, however, both provenances had surprisingly similar numbers of mature umbels (trait 14) despite the fact that the indigenous provenance bloom earlier. The plants of restored provenances produced more umbels in total (trait 12) and thus had their maximum number of flowering umbels later (trait 10 and 12). But at the end of the vegetation period not all of their umbels ripened, because autumn began with its cold and moist days. If climate change leads to a longer period of hot and dry summer days, the character of longer seed ripening, however, may become beneficial in the future. Seed production is probably the most common aspect to evaluate fitness, but the establishment of seedlings is nature's proof and we have not checked this in this study. We analysed only the measurable number of umbels with ripe fruits only (trait 14). Therefore, population recruitment and establishment in nature is limited by seedling survival rather than seed production. Additionally, it depends on the competitors in the field. In *Pulsatilla patens*, *Silene otites* and *S. chlorantha* (Lauterbach *et al.* 2011, 2012, Röder and Kiehl 2006) the authors mentioned a negative effect of cover by herbaceous plants and litter on seedlings. Seedling emergence and survival sometimes differ between species of the same habitat (Jakobsson and Eriksson 2000, Ryser 1993).

In a previous study, we tested the population genetic structures between indigenous and restored populations of *D. carota* in the same sites as studied here (Reiker *et al.* 2015). There we detected negligible genetic differentiation between indigenous populations and populations restored with non-local seed material. No negative effects on allelic richness, selective sweeps, or reduced genetic diversity within populations were observed, with only one exception in a study site, where inbreeding effects were presumed. However, there is a controversial discussion on quantitative genetics and fitness correlation, e.g. Lammi *et al.* (1999) could not detect any correlation between genetic diversity and reproductive fitness. These results are in contrast to the positive correlations between fitness and genetic diversity of *Gentianella germanica* (Fischer and Matthies 1998), *Cochlearia bavarica* (Paschke *et al.* 2002) and *Succisa pratensis* (Vergeer *et al.* 2003).

By testing several generative fitness parameters of *D. carota* we see an ambivalent outcome. The earlier genetic analysis (Reiker *et al.* 2015) did not support a regional provenance concept for restoration purposes, while slight differences in phenological parameters related to fitness pinpoint to 'mix and match-admixture provenancing' as a compromise strategy.

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Appendix 1. Four non-significant vegetative traits: origin (k = 2, indigenous or restored populations), the interaction of mowing and origin was neglected here. Abbreviation: df = degrees of freedom, MQ = sum of mean squares, F = variance ratio, *p* = error probability, significant *p*-values < 0.05 are written in bold. Traits are indicated by numbers in parentheses.

	length of the root (3)				diameter of the root (4)				weight of the leaves (fresh, 5)			
	df	MQ	F	*p*	df	MQ	F	*p*	df	MQ	F	*p*
Intercept	1	**1346.995**	**6248.198**	**< 0.001**	1	**3527.655**	**2770.244**	**< 0.001**	1	**456.1158**	**879.9536**	**< 0.001**
Origin	1	0.447	2.072	0.151484	1	0.060	0.047	0.827952	1	0.4656	0.8983	0.344294
Error	219	0.216			219	1.273			219	0.5183		

	weight of the roots (fresh, 7)			
	df	MQ	F	*p*
Intercept	1	**2391.982**	**253.3268**	**< 0.001**
Origin	1	7.824	0.8286	0.363682
Error	219	9.442		

Appendix 2. Continued from Appendix 1.

	number of fruiting umbels (13)				weight of ripe umbels (15)			
	df	MQ	F	*p*	df	MQ	F	*p*
Intercept	1	**15881.01**	**720.7**	**< 0.001**	1	**1605.49**	**377.2**	**< 0.001**
Origin	1	0.01	0.0	0.988	1	1.79	0.4	0.517
Error	350	22.03			350	4.26		

	duration from first flowering to highest amount of fruiting umbels (17)				number of simultaneously flowering or fruiting umbels (18)			
	df	MQ	F	*p*	df	MQ	F	*p*
Intercept	1	**4437498.28**	**3748.8**	**< 0.001**	1	**25317.31**	**818.1**	**< 0.001**
Origin	1	216.85	0.2	0.669	1	7.46	0.2	0.624
Error	342	1183.71			350	30.95		