

UDC 630*165.3:634.74+582.866

DOI: 10.17238/issn0536-1036.2018.5.26

GENETIC VARIATION IN GROWTH CHARACTERISTICS OF *HIPPOPHAE RHAMNOIDES* L. GROWN UNDER CONTROLLED CONDITIONS*

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The Sea Buckthorn (*Hippophae rhamnoides* L.), being one of the most useful plants in the food and medical industry, is widely used for field amelioration, soil recultivation and restoration of disturbed lands. Knowledge about genetic parameters for important traits is a prerequisite for a successful breeding of any species. There are limited number of publications on within-population variation for growth traits and frost hardiness of Sea buckthorn. The experiments were done under the controlled conditions in a climate chamber at the Department of Forest Genetics, Swedish University of Agricultural Sciences. Seedlings of Sea Buckthorn, originating from a controlled cross between three female plants and six male plants, as well as from an open pollination of mother plants, were grown under the controlled conditions until bud-set, a period of dormancy and an ensuing bud flush. Variation in growth, duration of growth period, earliness in bud flush and the fraction of frost-damaged buds after freezing were studied. Confirming previously reported observations, we found that Sea Buckthorn seedlings do not terminate growth at long nights, but low temperature treatment is needed. This lack of photoperiodic response stands in contrast to the majority of tree species in the temperate region. In this experiment, Sea Buckthorn reveals high level of genetic variance for growth and growth rhythm. The female variance component for the characteristics studied was higher than the male variance component, probably owing to seed size. The results analysis suggest that estimation of genetic parameters in Sea Buckthorn shall be based upon controlled crosses rather than on open pollinated progenies. The observed maternal effects indicate that seed weight may be a significant covariate in analyses of variance. The freezing test used in this experiment did not disclose any major genetic variance components responsible for the variation in fraction of damaged buds after freezing.

Keywords: Sea Buckthorn, genetics, controlled cross, open pollination, female and male plants, seedlings, growth, frost hardiness.

Introduction

The Sea Buckthorn (*Hippophae rhamnoides* L.) is known as a useful plant and in many countries of the world it has received increasing attention as a medicine plant with fruits, leaves and bark rich in different vitamins and other biologically active substances [10, 16]. It is an important source for essential food ingredients as well [18, 19]. Sea Buckthorn also has excellent nitrogen fixing properties, thus, it has a wide use for field amelioration, recultivation and for stabilizing sandy areas and slopes [23].

*Статья опубликована в рамках реализации программы развития научных журналов в 2018 г.

For citation: Demidova N.A., Eriksson G. Genetic Variation in Growth Characteristics of *Hippophae rhamnoides* L. Grown under Controlled Conditions. *Lesnoy Zhurnal* [Forestry Journal], 2018, no. 5, pp. 26–37. DOI: 10.17238/issn0536-1036.2018.5.26

Hippophae rhamnoides L. occurs over large areas of Europe and Asia, with two discrete distributions in Europe: one European coastal area which stretches along the Baltic and the North Sea, along the West coast of England and Ireland, along the East coast of Scandinavia and one Central European area, which is directly connected with the mountainous part of Asia [20]. It is a typical pioneer species that can rapidly colonize new areas. It forms extensive thickets in habitats where there is no competition from trees or other high vegetation [22]. The plants are sensitive to light conditions, and usually cannot grow under the shadow of other trees. The species is plastic to temperature and soil conditions [6].

Sea Buckthorn is the subject of a large-scale research, and therefore there is a huge amount of publications about its useful properties and use for medical, food, cosmetic and environmental purposes. Knowledge about genetic parameters for important traits is a prerequisite for a successful breeding of any species. There are many reports on among-population variation of markers in *Hippophaea rhamnoides* [8, 11, 23, 26, 29]. Jeppsson et al. [15] found more variation within Sea Buckthorn populations and a very little variation between populations, what they explained by differences in population sizes and/or the continuity in spatial distribution. Contrary to this, there is a few publications on within-population variation for growth traits and frost hardiness. There are some reports about variation among cultivars [14, 27]. Zemtsova [7], using the method of ISSR analysis for Sea Buckthorn varieties, determined the degree of genotypic diversity of seabuckthorn samples of different eco-geographical origin in the collection of the Lisavenko Research Institute of Horticulture for Siberia, which allowed to establish the degree of genetic similarity between different ecotypes, as well as the prospects of the biochemical potential of the seabuckthorn varieties. Shan [25] reported on parental mean heights of eight hybrids and their offspring heights. They estimated the regression coefficient between parent and offspring at 0.17, which in this case is an estimate of the heritability for tree height. The range of heights was 205–233 cm; no tree age was given. It was stated that most of the hybrids were taller than their parental means. Rousi [21] reported high variation for morphological traits in 46 seedling populations and in adult populations from Asia and Europe. Based on the observed large variation in morphology and growth rhythm he pointed out that the species must have a wide adaptability that can be exploited in breeding. Tang and Tigerstedt [28] reported low female heritability for winter damage, 0.04, while there were high heritability's for several flowering and fruit characteristics, even heritability's beyond the permitted 1.00 were reported. Their estimates were based on two sets of disconnected factorial matings between Finnish females and Danish males. One factorial being 3×8 and the other 5×6. Strong non-additive effects were noted for flowering and fruit traits. In a paper addressing the potential for *Hippophae rhamnoides* cultivation in the USA, results as regards growth and frost tolerance of 13 cultivars growing at the Russian Siberia experiment station were presented by Letchamo et al. [17]. At the age of five the tree height varied in the range 1.99 and 3.12 meters. All cultivars were characterized by high general and bud frost tolerance and limited variation among the cultivars.

Sea Buckthorn is a complicated species for breeding since hybridization and accompanying progeny evaluation are required. A major task for Sea Buckthorn breeding is to combine traits of resistance to harsh weather conditions with fruit quality traits. Absence of thorns is one of those quality traits, which play an essential role in its cultivars creation. In relation to the development of northern horticulture, there is need to widen the variety of available berry cultivars, suitable for cultivation under northern conditions [9]. A gene bank of *Hippophae rhamnoides* L.

with large diversity of qualitative and quantitative characteristics has been collected in the Arkhangelsk Dendrological Garden since 1969. The results from the initial test under Dendrological Garden conditions gave guidelines for transferring the plant material to the North [9], but it was found that in some years there was a high mortality, which could be attributed to damage of the root systems in mild winters with much snow. Eliseev [3] concluded that successful introduction of Sea Buckthorn is not possible without improvement of winter hardiness and frost tolerance.

Frost damage of many tree species is frequently attributed to a growth rhythm unsuitable for the growth conditions such that plants in frost sensitive phases are exposed to late spring frosts or early autumn frosts, alternatively to both of them [13]. It is plausible that *Hippophae rhamnoides* L. plants transferred over wide distances to new and different growth conditions will suffer from maladaptation of the growth rhythm. Nilov [5] reported that growth cessation in Sea Buckthorn is triggered by low temperatures. This contrasts with the response to long nights of many tree species from the temperature zone [12]. Under temperate climatic conditions, there is usually a clinal variation for this response such that northern populations require a shorter night than southern populations for bud-set and growth cessation [12]. It would be useful for future breeding to clarify whether *Hippophae rhamnoides* L. constitutes a deviating species to the general pattern of triggering of growth cessation by long nights. Such study must be done under strictly controlled conditions.

Published information concerning the genetic parameters for quantitative traits in *Hippophae rhamnoides* L. is limited. The goal of the present study is to examine the genetic variation in a number of characteristics of adaptive importance of sea buckthorn hybrids, by growing seedlings under the controlled climatic conditions in a growth chamber. The characteristics are height growth, number of days to achieve 90 % of total growth (D90), earliness in flushing and degree of bud damage caused by frost. In addition, variation in quality characteristics such as stem straightness and number of thorns were assessed.

Research Methodology

The seeds for the study originated from a 3×6 factorial mating carried out in the Arkhangelsk Dendrological Garden. Seventeen of these 18 families had seeds enough for our experiment. The three females of *H. rhamnoides* L. spp. *mongolica* were selected in Siberia (Khakasiya) and the six males *H. rhamnoides* L. spp. *rhamnoides* were selected in the Åland archipelago, Finland. In addition, open-pollinated seeds from the three females were included in the experiment. The Siberian female plants are characterized by large fruit size, absence of thorns but low frost tolerance under Arkhangelsk weather conditions. The Finnish male plants are characterized by good winter hardiness, but high thorniness and small fruits.

Experiments were done under the controlled conditions in the climate chamber at the Department of Forest Genetics, Swedish University of Agricultural Sciences. The cultivation conditions are given in Table 1. After germination, the seedlings were transplanted to pots and were randomized in a block design, 10 blocks×32 seedlings. A second transplanting to larger pots took place after 10 weeks.

Plant height had been measured once a week after the first transplantation of the seedlings and three times a week after the second transplantation. The amount of days to reach 90 % of final height was interpolated from the individual growth curves.

The stage of bud flushing during the second growth period had been assessed every day after plants were transferred to continuous light, using a scale, where: 0 – dormant bud; 1 – buds slightly swollen; 2 – buds swollen, scales still closed, brown-green; 3 – burst of bud scales, tips of leaf emerging; 4 – leaf emerging from the buds and shoot growing; 5 – leaf elongation; 6 – full leaf, new buds developing.

Table 1

Cultivation conditions and subdivision of the first growth period into sub-periods

Period	Cultivation conditions			
	Week no.	Night length (h)	Temperature (°C)	
			day	night
Germination	1–2	0	20	20
	<i>Transplantation 1¹</i>			
Sub-period 1 beginning	3–5	0	20	20
	6	3	20	20
	7–10	Gradual increase of night by 1h/week until 11 h night	20	20
	<i>Transplantation 2²</i>			
Sub-period 2 beginning	11–14		20	20
Growth cessation	15–19		20	10
	20–21		10	10
Dormancy period	22	16	4	4
	23–26	16	2	2
Breaking of dormancy and bud flushing	27–30	8	20	10

¹A first transplantation was done during the first days of week 3.

²A second transplantation to larger pots was done during the first days of week 11.

Freeze testing was carried out during week 20. One lateral shoot from eight plants of each family were cut and put into separate plastic bags, where they remained sealed throughout the testing. This freeze testing of shoots was performed in darkness in freezing chamber under different conditions, at -7 °C and -17 °C respectively. Control plants were kept at $+4$ °C. The treatment started from $+10$ °C and then the temperature was slowly reduced by $+3$ °C per hour until final temperature was reached. It was being maintained for four hours. After the freeze treatment temperature was gradually increased to $+10$ °C. The shoots were stored at $+10$ °C during three days and then visual frost damage was assessed by counting damaged buds. Since no damage was induced by $+4$ °C, only data from -7 °C and -17 °C were included in the analysis of variance. A separate analysis of bud damage for the -17 °C treatment alone was carried out, as well.

The quality characteristics like thorniness, number of lateral shoots and stem straightness were assessed at the end of the experiment. The following scales and methods were used

- stem straightness was estimated after growth cessation, in grades from 1 to 3, where 1 – straight, 2 – slightly curved and 3 – curved;
- presence of thorns was recorded according to a scale, where: 0 – no thorns, 1 – single thorns, 2 – several thorns;
- the number of lateral shoots was recorded since it is connected with thorn presence. The more lateral shoots, the higher thorniness.

Statistical methods

Analyses of variance were used to estimate causes of variation in individual characteristics according to the following model:

$$Y = \mu + b_j + f_k + m_l + (f \times m)_{kl} + e_{ijkl},$$

where: Y – individual plant value;

μ – population mean;

b_j – effect of box ($j = 1, \dots, 10$) ($J = 1, \dots, 20$ after second transplantation);

f_k – effect of female ($k = 1, \dots, 3$);

m_l – effect of male ($l = 1, \dots, 6$);

$(f \times m)_{kl}$ – interaction female \times male;

e_{ijkl} – residual error.

When frost damage was analyzed, effect of treatment was included in the model:

$$Y = \mu + t_i + b_j + f_k + m_l + (f \times m)_{kl} + (b \times f \times m)_{jkl} + (t \times f)_{ik} + (t \times m)_{il} + (t \times f \times m)_{ikl} + e_{ijkl},$$

where: t_i – treatment ($I = 1, \dots, 2$);

$(b \times f \times m)_{jkl}$ – interaction box \times female \times male;

$(t \times f)_{ik}$ – interaction treatment \times female;

$(t \times m)_{il}$ – interaction treatment \times male;

$(t \times f \times m)_{ikl}$ – interaction treatment \times female \times male.

Variance components were estimated using the same model, with all effects except treatment considered to be random. SAS statistical package [24] was used for the GLM and VARCOMP procedures.

Results

Figure 1 illustrates the large variation among females and males as regards mean percentage of damaged buds after freeze testing at -7°C . The family performance as regards bud damage after freeze testing at -17°C caused significantly higher frost damage than exposure to -7°C .

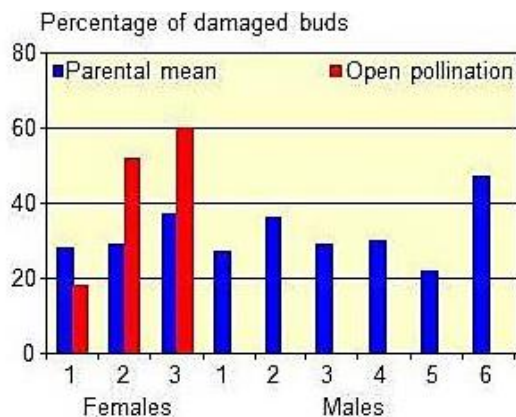


Fig. 1. Mean percentage damaged buds after freeze testing at -17°C of 18 full-sib families from a 3×6 factorial mating as well as mean percentages for open pollination of the three female clones included in the mating

Regression analysis showed that there was a weak, non-significant relationship between date of growth cessation and frost damage. Figure 2 and Table 2 reveal that the additive variance components (CV_A) for females were mostly large for growth and phenology traits. There was a significant female \times male interaction for several traits. All CV_A s for frost damage after exposure to -17°C were close to zero. Bud flushing was recorded at five occasions, and it showed significant female differences except one occasion. The largest variance component was obtained at

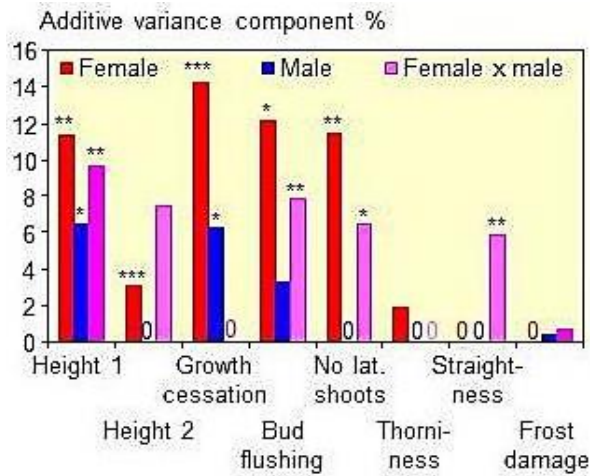


Fig. 2. Additive variance components estimates for female, male, and female × male interaction in the growth chamber study of a 3×6 factorial mating

Table 2

Mean values for bud damage (−17 °C)

		Male clones						Open pollination
		1	2	3	4	5	6	
Female clones	1	0.202		0.000	0.376	0.510	0.386	0.176
	2	0.378	0.288	0.312	0.172	0.635	0.439	0.601
	3	0.230	0.293	0.365	0.360	0.274	0.241	0.516

the end of flushing, amounting to 25.1 %. There was also a large time variation of bud flushing between families. Generally, the female variance components were a few times larger than both the male and the female × male components.

Little or no genetic influence could be detected for the quality characteristics – thorniness, number of lateral shoots and stem straightness.

Discussion

It is important to point out that this is a pilot experiment with Sea Buckthorn under the controlled conditions which has not been done before. Our results confirm the observations made by Nilov [5], that long nights do not trigger the growth cessation in *Hippophae rhamnoides* L. To obtain growth cessation, the plants must be exposed to low temperature. This is a contrast to the statement by Rousi [21] that “the termination of activity in the fall took place in the exact order from north to south”, which means that a photoperiodic triggering is important for growth cessation. Our observation also contrasts with the majority of other tree species from the temperate zone as stated in the introduction. A provenance study under strictly controlled conditions would be useful to get an unequivocal answer to the roles of photoperiod and temperature for growth cessation.

The material selected for this study is a limited sample of the present breeding stock of *Hippophae rhamnoides* L. because of practical limitations. Nevertheless, a significant genetic variation in several characteristics was detected. In spite of the lower number of females than males the variance component for the female was for most traits a few times larger than the male effect (Table 2 and Figure 2). This suggests that there is a strong maternal effect in these young plants and the true

genetic female variance component is presumably far less than shown in Figure 2. This is supported by the large drop of the female variance component for plant height from sub-period 1 to sub-period 2. This maternal effect is supposed to originate from the rather large seed size. If our interpretation is correct, it also suggests that open pollinated progenies will not give good estimates of genetic parameters. Based on our data, genetic parameters should be obtained from mating, in which a few females are mated to a large number of males and the genetic parameters should be exclusively derived from the males. Alternatively, individual seed weights must be recorded and used as covariates in the parameter estimations, which though is labor demanding.

The early study of genetic differences in winter hardiness of Sea Buckthorn was done in the Arkhangelsk Dendrological Garden with a limited amount of material [2]. However, there were significant female and male effects for this characteristic, but the main factor which had strong influence on frost tolerance was winter conditions. In the present study, we were unable to detect any significant genetic effect of frost tolerance after growth cessation. Neither did a regression analysis show any significant relationship between point of time for growth cessation and frost damage.

Besschetnov [1] reported that bud flushing in Sea Buckthorn was under genetic control. He reported about big differences in flushing in plants from different provenances. The significant genetic influence on bud flushing in our study confirms his conclusion.

We did not detect any genetic influences on thorniness ability. However, Kalinina and Panteleeva [4] pointed out that usage of highly thorny plants in hybridization gives a thorny progeny, thus suggesting dominance for this trait.

Presence of lateral annual shoots makes fruit harvesting difficult. This trait correlates with thorniness [4]. In this study we detected significant female and family genetic effect on variation of this quality characteristic.

Our data suggest that it is worthwhile to carry out more comprehensive mating to get more precise estimates of genetic parameters. Such estimates are needed for an efficient breeding of *Hippophae rhamnoides* L.

The number of parents is far too low to allow any precision in estimates of genetic correlations between different traits. Such estimates are indispensable for an efficient breeding program for any species.

Conclusion

The results of the present study indicate that Sea Buckthorn seedlings do not terminate growth at long nights, but low temperature treatment is needed. This lack of photoperiodic response stands in contrast to the majority of tree species in the temperate region. In this experiment, Sea Buckthorn reveals high estimates of genetic variance for growth and growth rhythm. The female variance component for the characteristics studied was higher than the male component, probably owing to influence from maternal inheritance and seed size. The results suggest that estimation of genetic parameters in Sea Buckthorn shall be based upon controlled crosses rather than on open pollinated progenies. The observed maternal effects indicate that seed weight may be a significant covariate in analyses of variance. The freezing test used in this experiment did not disclose any major genetic variance components responsible for variation in fraction of damaged buds after freezing.

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Received on August 16, 2018

УДК 630*165.3:634.74+582.866

DOI: 10.17238/issn0536-1036.2018.5.26

ГЕНЕТИЧЕСКАЯ ИЗМЕНЧИВОСТЬ РОСТОВЫХ ХАРАКТЕРИСТИК ОБЛЕПИХИ КРУШИНОВИДНОЙ (*HIPPOPHAE RHAMNOIDES* L.) ПРИ ВЫРАЩИВАНИИ В КОНТРОЛИРУЕМЫХ УСЛОВИЯХ

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Облепиха (*Hippophae rhamnoides* L.), одно из самых полезных растений для пищевой и медицинской промышленности, широко используется для улучшения почвенного плодородия и рекультивации нарушенных земель. Знание генетических параметров важнейших признаков любых видов растений является предпосылкой успешной селекции. Существует ограниченное количество публикаций по внутривидовой изменчивости облепихи по признакам роста и морозостойкости. Эксперименты проводились в контролируемых условиях климатической камеры на кафедре лесной генетики Шведского университета сельскохозяйственных наук. Сеянцы облепихи, полученные от контролируемого скрещивания между тремя женскими растениями и шестью мужскими растениями облепихи, а также сеянцы от свободного опыления материнских растений, выращивались в контролируемых условиях до перехода их в период покоя и последующего распускания почек. Изучались изменения в росте, длительность периода роста, раннее распускание почек и степень их повреждения морозом. В подтверждение предыдущих сообщений, нами обнаружено, что завершение роста побегов облепихи обусловлено в основном тепловым фактором. Отсутствие реакции облепихи на фотопериодичность отличает ее от большинства древесных видов умеренного пояса. В ходе эксперимента установлен высокий уровень генетической дисперсии для показателей роста у облепихи. Компонент женской дисперсии для изученных показателей был выше, чем мужской, вероятно из-за размера семян. Анализ результатов выявил, что оценка генетических параметров облепихи должна проводиться на потомстве от контролируемых скрещиваний, а не от свободного опыления. Наблюдаемый материнский эффект показал, что вес семян может быть значительной ковариатой при дисперсионном анализе. Тест на замораживание, проведенный в этом

Для цитирования: Demidova N.A., Eriksson G. Genetic Variation in Growth Characteristics of *Hippophae rhamnoides* L. Grown under Controlled Conditions // Лесн. журн. 2018. № 5. С. 26–37. Itstic. DOI: 10.17238/issn0536-1036.2018.5.26

эксперименте, не выявил каких-либо компонентов генетической дисперсии, ответственных за изменение доли поврежденных почек после замораживания.

Ключевые слова: облепиха, генетика, контролируемое скрещивание, свободное опыление, женские и мужские растения, рост, морозоустойчивость.

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Поступила 16.08.18