



Impact of Heated, Acidified Volcanic Ash and Manures on Properties of Marginal Soil and Growth of Soybean

Khusrizal¹, Basyaruddin², M.S. Rahayu², R. Pradipta², Nasruddin¹

10.18805/IJArE.A-593

ABSTRACT

Background: The nutrients released from volcanic ash and manures can enhance soil fertility and plant growth. Weathering of minerals in volcanic ash depends on water, temperature and acids. This study aims to examine the influence of heated and acidified volcanic ash and their combination with manures on pH and nutrient levels of marginal soil and soybean growth.

Methods: The study was designed using a factorial Randomized Block Design, consisted of two factors with three replications. The first factor was heated and acidified volcanic ash (VA) and the second factor was cow manures (CM) which consist of three levels.

Result: The results showed that various of VA treatment, as well as its combination with CM on marginal soils exhibited acidic soil pH, Total-N, exchangeable-K, -Ca were low, while available P and exchangeable-Mg were classified moderate. Various treatments of VA and their combination with CM did not significantly interact on all parameters, except some parameters of soybean. Application of VA and CM on marginal soil interacted significantly on plant height and weight of 100 grains only.

Key words: Mineral weathering, Nutrients availability, Organic matter, Soybean growth, Volcanic ash.

INTRODUCTION

In Indonesia, soybean (*Glycine max* L. Merrill) is classified as the third largest crop after rice and corn. It is economically the most important bean which widely used for human consumption, industrial products and the animal feed industry. Therefore, the demand of this legume is increasing time to time. Consumption of soybean in Indonesia is reaching 2.2 million ton per year and tend to increase, while the production of this crop is still insufficient, less than 1 ton per year (Roessali *et al.* 2017). In 2016, its production has been estimated to increase from 1.1 million ton to 1.7 million ton in 2020. Unexpectedly, the production was increased rapidly from 2.2 million ton in 2016 to 2.6 million ton in 2020 (Ningrum *et al.* 2018). The efforts to enhance soybean production in Indonesia have been done in many ways including the utilization of potential marginal soil through soil quality improvement using basic principle of sustainable land use management (Hasan *et al.* 2015).

Area under marginal soil in Indonesia reaches up to 157.2 million ha. Quality of this marginal soil has been done in various ways, such as application of organic and inorganic fertilizers. Volcanic ash is one of the inorganic fertilizers which could be applied to improve the soil. This material is easy to find in Indonesia as this country is known to have great number of volcanoes (Latif *et al.* 2016). There are some active volcanoes in Sumatra Utara Province. Mount Sinabung is one of them. After a 400-year dormancy, it has been erupted in 2010 and it has been continuously active until now. The volcanic ash materials ejected from the volcano rejuvenates soil and provides nutrients reserve, resulted in quality improvement of soil and crop yield (Ramos *et al.* 2014; Minami *et al.* 2016). Rapid decomposition of minerals from volcanic ash releases nutrients required by the crop. It required more than 15 years for these minerals to decay (Khusrizal *et al.* 2018). Volcanic ash weathered

¹Program Study of Agroecotechnology, Faculty of Agriculture, Universitas Malikussaleh, Aceh Utara, 24355, Aceh, Indonesia.

²Program Study of Agrotechnology, Faculty of Agriculture, Universitas Islam Sumatera Utara, Medan, 20217, Indonesia.

Corresponding Author: Khusrizal, Program Study of Agroecotechnology, Faculty of Agriculture, Universitas Malikussaleh, Aceh Utara, 24355, Aceh, Indonesia. Email: khusrizal@unimal.ac.id

How to cite this article: Khusrizal, Basyaruddin, Rahayu, M.S., Pradipta, R. and Nasruddin (2021). Impact of Heated, Acidified Volcanic Ash and Manures on Properties of Marginal Soil and Growth of Soybean. Indian Journal of Agricultural Research. 55(2): 202-206. DOI: 10.18805/IJArE.A-593.

Submitted: 24-08-2020 **Accepted:** 10-10-2020 **Online:** 16-01-2021

rapidly under the influence of high temperature, water and acids (Tan, 2011).

On the other hand, organic matter (OM) ameliorant possessed the ability to enrich the soil and to accelerate mineral decomposition by producing organic acids (Beedy *et al.* 2010). This organic matter improved the soil quality through enhancement of soil physical, chemical and biological properties (Joshi *et al.* 2016; Orji and Eke, 2018; Singh *et al.* 2019). Suriadikusumah *et al.* (2013) reported that the combination of volcanic ash, manure and inceptisol soil contributed to the increase of C-organic, Total-N and also the growth of maize. The information about rapid mineral weathering in volcanic ash accelerated by heated decomposer, acids and manure is still scanty. Therefore, this study was conducted to evaluate the influence of application of heated and acidified volcanic ash combined with cow manure on quality improvement of marginal soil and soybean growth.

MATERIALS AND METHODS

The research was carried out using polybags in Experimental Garden of Agriculture Faculty, Universitas Islam Sumatra Utara, Medan, Indonesia, from August to November 2017. The materials used were volcanic ash, marginal soil, cow manure, seeds of hybrid soybean and polybags (30x30 cm). The tools used were machete knife, measuring tape, pan, kitchen knife, hoe, hand sprayer, oven and analytical balance.

The volcanic ash was obtained from Mount Sinabung, Karo Regency, Sumatra Utara, Indonesia (3°11'27.1"N, 98°24'52.1"E), collected from the depth 0-10 cm of soil surface, characterized by soft structure and grey in colour. The marginal soil, ultisols was provided from Experimental Garden of Agriculture Faculty, Universitas Islam Sumatera Utara, characterized by yellowish colour. This soil (thickness 10 cm) was collected in composite basis, where the top soil was replaced to reach the sub soils. The soils were then dried in room temperature and were sieved using sieve 2 mm. The cow manure (CM) applied were the composted and odorless manure which has been obtained through proper processing. The soybean seeds used in this research was hybrid P32.

Randomized block design factorial was employed in this research, where it had two factors. The first factor was volcanic ash (VA) with 4 different heating treatments: VaO (pure volcanic ash without treatment), VaH (oven-heated volcanic ash at 100°C), VaB (water heated volcanic ash at 100°C) and VaA (acidified volcanic ash using HCl 0.01 N). The second factor was cow manure (CM) with 3 different doses: CM0 (0 g/polybag), CM50 (50 g/polybag), CM75 (75 g/polybag). It had 12 experimental units, replicated 3 times totally 36 experimental units.

VA heating : (i) VA was placed into oven and was heated for 6 hours at 100°C. It was then cooled in a closed room to avoid direct air exposure, (ii) VA with a dose of 2 kg and 1 liter of water was stirred until it becomes sludge, then boiled it for 6 hours at 100°C, then cooled in a closed room. VA acidification: VA acidification was performed by adding 1 liter/2 kg VA of 0.01 N HCl solution. Stirred evenly in a pot (60 x 40 cm), left for 6 hours in a closed room. Two weeks before the soybean seedlings were planted, 10 kg of soil was filled in each polybag and added VaO, VaH, VaB and VaA, respectively 113, 109.5, 108.5, 116 g/polybag and CM 0, 50, 75 g/polybag and stirred evenly.

Sowing of two selected soybean seeds was carried out into planting holes and were then covered with soil and later thinned to one plant/polybag. Cultural practices viz., watering and plant protection measures were monitored properly.

The variables observed in the soil were soil pH, Total-N, available P, K-, Ca- and exchangeable Mg. The measurements of soil pH (w/s:2.5/1) using pH meter (model WTW 330i/Germany), determination of Total-N (Kjeldahl), available P (Bray) through extraction NH_4F 0.03 N + HCl 0.025 N (Spectrophotometer-UV.vis), exchangeable

K through extraction NH_4OAc pH 7.0 (Flame photometer-Model 410), while Ca and exchangeable Mg with extraction NH_4OAc pH 7.0 (Atomic Adsorption Spectrophotometer-Model AA 220) were recorded. The variables observed in the plant samples were plant height, number of productive branches, number of pods per plant, pod weight per sample, weight of 100 seeds, root weight and active root nodules per plant. The percentage of active and inactive nodules were examined after harvest by cutting them in half (the active nodules were pink in colour) and were calculated using formula:

$$\frac{\text{Active nodules}}{\text{Inactive nodules} + \text{Active nodules}} \times 100\%$$

The results of data analysis of soil properties and volcanic ash were determined based on categorization of soil chemical properties analysis (Hardjowigeno, 2010). F Test and Duncan's Multiple Range Test (DMRT) with probability level 5% were assessed

RESULTS AND DISCUSSION

Determination of soil pH and macro nutrient

Table 1 described the effect of application of VA and CM on soil pH and macro nutrient in marginal soil. The results revealed that the soil possessed low pH (acid soil), low concentrations of Total-N, exchangeable K and exchangeable Ca. However, it registered moderate available P and exchangeable Mg contents. (Hardjowigeno, 2010). There was no significant results on those variables before and after application of VA and CM, except for exchangeable Mg which increased from low to moderate. Insignificant soil pH was caused by the application of acidic VA. Geologically, Mount Sinabung is ejected two types of rocks, plio-pleistocene (andesitic rocks) and quaternary-aged (sedimentary rocks) (Kusumayudha *et al.* 2018). Those two type of rocks contain high SiO_2 (65%) (Dumroese *et al.* 2007). CM also contains organic acids which inhibits soil pH to increase (Lakshmi *et al.* 2011). The minerals in VA applied in this research also did not weather optimally, due to no mineralization of nutrients (K, Ca, Mg) resulted in insignificant soil pH.

Soil pH, Total-N, available P, exchangeable K, exchangeable Ca and exchangeable Mg were higher in treated soils compared to untreated soils. The highest soil pH was demonstrated by the application of VaB and CM75. For Total-N, available P, exchangeable K, exchangeable Ca and the highest exchangeable Mg were obtained in the soil applied VaA and CM75. It indicated that VaB or VaA and CM were the best combination applied on plants compared to untreated ones. Exchangeable Mg itself, increased from low ($0.61 \text{ cmol kg}^{-1}$) to moderate ($1.00\text{-}1.32 \text{ cmol kg}^{-1}$) after the application of VA and CM. This condition is linked to the amount of easily weathering mineral hyperstene as a main source of Mg which is present abundantly in VA Sinabung. The another source is from hornblende mineral which also found in the VA Sinabung (Khusrizal *et al.* 2018). Mitchell

Table 1: Influence of VA and CM on pH level and macro element content of marginal soil.

Treatment	pH	Tot-N	Av-P	Exc-K	Exc-Ca	Exc-Mg
Volcanic ash (VA)						
VaO	5.33 [^]	0.12 ⁺	15.70 ⁺⁺	0.13 ⁺	4.17 ⁺	1.07 ⁺⁺
VaH	5.34 [^]	0.12 ⁺	15.67 ⁺⁺	0.14 ⁺	4.19 ⁺	1.10 ⁺⁺
VaB	5.36 [^]	0.13 ⁺	15.81 ⁺⁺	0.15 ⁺	4.29 ⁺	1.17 ⁺⁺
VaA	5.31 [^]	0.14 ⁺	15.90 ⁺⁺	0.14 ⁺	4.33 ⁺	1.23 ⁺⁺
Cow manure (CM)						
CM0	5.30 [^]	0.11 ⁺	15.48 ⁺⁺	0.12 ⁺	4.10 ⁺	1.00 ⁺
CM50	5.34 [^]	0.13 ⁺	15.78 ⁺⁺	0.14 ⁺	4.24 ⁺	1.18 ⁺⁺
CM75	5.37 [^]	0.15 ⁺	16.04 ⁺⁺	0.16 ⁺	4.40 ⁺	1.24 ⁺⁺
Combined treatment						
VaOCM0	5.28 [^]	0.10 ⁺	15.39 ⁺⁺	0.11 ⁺	4.02 ⁺	0.92 ⁺
VaOCM50	5.33 [^]	0.12 ⁺	15.71 ⁺⁺	0.13 ⁺	4.19 ⁺	1.12 ⁺⁺
VaOCM75	5.37 [^]	0.15 ⁺	16.02 ⁺⁺	0.16 ⁺	4.32 ⁺	1.18 ⁺⁺
VaHCM0	5.28 [^]	0.11 ⁺	15.41 ⁺⁺	0.12 ⁺	4.07 ⁺	0.97 ⁺⁺
VaHCM50	5.34 [^]	0.12 ⁺	15.62 ⁺⁺	0.15 ⁺	4.18 ⁺	1.14 ⁺⁺
VaHCM75	5.39 [^]	0.14 ⁺	15.97 ⁺⁺	0.13 ⁺	4.33 ⁺	1.21 ⁺⁺
VaBCM0	5.31 [^]	0.12 ⁺	15.53 ⁺⁺	0.16 ⁺	4.14 ⁺	1.03 ⁺
VaBCM50	5.36 [^]	0.14 ⁺	15.84 ⁺⁺	0.15 ⁺	4.28 ⁺	1.21 ⁺⁺
VaBCM75	5.41 [^]	0.15 ⁺	16.07 ⁺⁺	0.11 ⁺	4.47 ⁺	1.28 ⁺⁺
VaACM0	5.32 [^]	0.12 ⁺	15.61 ⁺⁺	0.13 ⁺	4.18 ⁺	1.11 ⁺⁺
VaACM50	5.34 [^]	0.14 ⁺	15.97 ⁺⁺	0.14 ⁺	4.31 ⁺	1.26 ⁺⁺
VaACM75	5.29 [^]	0.16 ⁺	16.12 ⁺⁺	0.17 ⁺	4.51 ⁺	1.32 ⁺⁺

Note: [^]acid; ⁺low; ⁺⁺medium; tot-N (%), av-P (mgkg⁻¹), exc-K (cmolk⁻¹), exc-Ca (cmolk⁻¹), exc-Mg (cmolk⁻¹).

Table 2: Effect of VA and CM on soybean growth.

Treatment	Cow manure			The mean
	CM0	CM50	CM75	
Volcanic ash				
Number of productive branches				
VaO	3.33	4.67	5.00	4.33
VaH	4.00	4.00	4.00	4.00
VaB	3.67	4.00	4.33	4.00
VaA	5.00	4.67	5.00	4.89
The mean	4.00	4.37	4.58	
Number of pods per plant				
VaO	147.50	119.67	109.67	125.61
VaH	83.67	94.00	107.33	95.00
VaB	83.67	94.00	107.33	95.00
VaA	128.67	107.33	116.00	117.33
The mean	110.88	103.75	110.08	
Weight of pod per sample (g)				
VaO	35.00	51.33	51.00	45.78
VaH	45.33	44.33	36.00	41.89
VaB	50.00	46.33	41.33	45.89
VaA	60.33	43.33	48.33	50.67
The mean	47.67	46.33	47.17	
Root weight (g)				
VaO	11.00	16.67	12.67	13.44
VaH	17.00	12.33	17.00	15.44
VaB	12.33	12.00	10.67	11.67
VaA	12.67	11.67	12.33	12.22
The mean	13.25	13.17	13.17	
Active root nodules per plant (%)				
VaO	30.65	27.67	28.19	28.91
VaH	20.38	22.00	18.76	20.38
VaB	22.43	25.97	20.15	22.85
VaA	27.15	21.40	28.89	25.81
The mean	25.15	24.32	24.00	

Table 3: Effect of VA interactions and CM on plant height and weight of 100 grains of soybean.

Treatment	Cow manure			The mean
	CM0	CM50	CM75	
Volcanic ash				
Plant heigth (cm)				
VaO	25.10aA	36.07bB	29.97aAB	30.38
VaH	27.73abA	28.03aA	37.83bB	31.20
VaB	35.03bA	29.30abA	33.63abA	32.66
VaA	24.30aA	32.80abB	40.10bB	32.40
The mean	28.04Q	31.55QR	35.38R	
Weight of 100 grains (g)				
VaO	11.33aA	12.33bB	13.00aB	12.44
VaH	12.00aA	11.67abA	13.00aA	12.22
VaB	13.67bB	11.00aA	13.00aB	12.56
VaA	12.33abA	12.00abA	11.67aA	12.00
The mean	12.33	11.92	12.67	

Note: - Numbers followed by the same uppercase letters in the same row and the same lowercase letters in the same column are not significantly different at the 5% level based on the DMRT Test (Duncan Multiple Range Test).

and Soga (2005) confirmed that Mg was formed from primary weathered minerals such as olivine, pyroxene and biotite contents of VA.

Soil pH and macro nutrient in marginal soil was found to be higher due the application of VA and CM combination compared to soil applied with VA alone. It revealed that the heated and acidified VA combined with CM demonstrated rapid mineral weathering, contributed to rapid release of nutrients. Primary minerals often experiences acidolysis and hydrolysis reactions, where these reactions play an important role in mineral weathering (Tan, 2011). In this research, the minerals of VA were not optimally weathered, caused by limited duration of heating and acidifying processes (6 hours). Besides, the unnatural condition affected this process. Gordon (2005) stated that fast weathering was created from natural physical, chemical and biological processes occurred in environment in the same time.

Growth and yield of soybean

The application of VA alone gave non-significant result on all variables observed in soybean and the application of CM significantly increased the plant height only. The combination of VA and CM significantly improved the plant height and weight of 100 seeds. Even though this combination did not exhibit significant results to the growth parameters of the crop it showed an increasing result on each variable observed. Number of productive branches, pods per plant and active root nodules were increased by the application of acidified VaA and CM75, while the highest number of pods per sample was found in plants applied with acidified VaA and CM0 and highest root weight was shown by the application of oven-heated VaH and CM75 (Table 2). These results indicated that there were an improvement in the soybean crop growth parameters attributed by the application of these materials even though it was insignificant. These results of experiments also indicated that heated and acidified volcanic ash established faster

nutrient release compared to other experiments. When plants obtains more nutrient even though it is inadequate, the plants are still be able to develop themselves (McGrath *et al.* 2013; Keino *et al.* 2015), on the other hand, nutrient balance is important in growth and development of plants, including soybeans (Changkija and Gohain, 2018). The combination of VA and CM gave significant interaction on plant height with application of acidified VaA and CM75 and weight of 100 seeds applied with water-heated VaB and CM0 (Table 3). These results revealed that the heated and acidified VA combined with CM significantly improved the plant growth.

Macro nutrients N, P, K, Ca and Mg has played their roles in supporting the plant development. These nutrients facilitate the root development, plant cells and also the development of plants in vegetative stage (White and Broadley, 2003). The development of plant cells is related to plant height, seed weight and leaf width (Razaq *et al.* 2017).

CONCLUSION

VA Sinabung and CM possessed low pH (acidic pH), low Total-N, exchangeable K and exchangeable Ca, while available P and exchangeable Mg were in moderate category. Oven and water heated VA (at 100°C) and acidified VA (with HCl 0.01 N) did not increase the soil pH, Total-N, available P, K-, Ca- and exchangeable Mg in each VA treatment. Also, heated and acidified VA applied onto marginal soil also exhibited non-significant results to soil pH, Total-N, available P, exchangeable K and exchangeable Ca, except for exchangeable Mg which increased from low to moderate. The mixture of VA and CM in soybean plant also revealed insignificant results on number of productive branches, pod number per plant, pod weight per sample, root weight and root nodules per plant. However, these combination increased the plant height and weight of 100 seeds. The results have proved that duration and environment play important role in mineral weathering.

REFERENCES

- Beedy, T.L., Snapp, S.S., Akinnifesi, F.K. and Sileshi, G.W. (2010). Impact of *Gliricidia sepium* intercropping on soil organic matter fractions in a maize-based cropping system. *Agriculture Ecosystems and Environment*. 138: 139-146.
- Changkija, S. and Gohain, T. (2018). Effect of organic nutrient sources on productivity of soybean [*Glycine max* (L.) Merrill]. *Agricultural Science Digest*. 38(1): 36-39.
- Dumroese, D.P., Miller, R., Mital, J., McDaniel, P. and Miller, D. (2007). Chemical change induced by pH manipulations of volcanic ash-influence soil Paper presented at the volcanic ash derived forest soils of the Inland Northwest: Properties for Implication Management and Restoration. Fort Collin Co. USDA.
- Gordon, S.J. (2005). Effect of environmental factors on the chemical weathering of plagioclase in hawaiian basalt. *Physical Geography*. 26(1): 69-84.
- Hardjowigeno, S. (2010). *Ilmu Tanah (Soil Science)*. Jakarta.: Akademi Pressindo.
- Hasan, N., Suryani, E. and Hendrawan, R. (2015). Analysis of soybean production and demand to develop strategic policy of food self-sufficiency: a system dynamics framework. *Procedia Computer Science*. 72: 605-612.
- Joshi, D., Gediya, K.M., Patel, J.S., Birari, M.M. and Gupta, S. (2016). Effect of organic manures on growth and yield of summer cowpea [*Vigna unguiculata* (L.) Walp] under middle Gujarat conditions. *Agriculture Sciences Digest*. 36(2): 134-137.
- Keino, L., Bajjukya, F., Ng'etich, W., Otinga, A.N., Okalebo, J.R., Njoroge, R. and Mukalama, J. (2015). Nutrients limiting soybean (*Glycine max* L.) growth in acrisols and ferralsols of Western Kenya. *PLoS One*. 10(12): e0145202.
- Khusrizal, Basyaruddin, Rambe, R.D.H. and Setiawan, I. (2018). Study of mineralogy composition, total and exchangeable content of K, Ca, Mg of volcanic ash from Sinabung Mountain eruption in North Sumatera, Indonesia. Paper presented at the Proceeding of Micoms 2017. Lhokseumawe.
- Kusumayudha, S.B., Lestari, P. and Paripurno, E.T. (2018). Eruption characteristic of the sleeping volcano, Sinabung, North Sumatera, Indonesia and SMS gateway for disaster early warning system. *The Indonesian Journal of Geography*. 50(1): 70-77.
- Lakshmi, C.S.R., Sreelatha, T., Rani, T.U., Rao, S.R.K. and Naidu, N.V. (2011). Effect of organic manures on soil fertility and productivity of sugarcane in north coastal zone of Andhra Pradesh. *Indian Journal Agricultural Research*. 45(4): 307-313.
- Latif, D.O., Rifa'i, A. and Suryolelono, K.B. (2016). Chemical characteristics of volcanic ash in Indonesia for soil stabilization: morphology and mineral content. *International Journal of Geomate*. 11(26): 2606-2610.
- McGrath, C., Wright, D., Mallarino, A.P. and Lenssen, A.W. (2013). Soybean Nutrient Needs. *Agriculture and Environment Extension Publications*. 189: http://lib.dr.iastate.edu/extension_ag_pubs/189.
- Minami, Y., Imura, T., Hayashi, S. and Ohba, T. (2016). Mineralogical study on volcanic ash of the eruption on September 27, 2014 at Ontake volcano, central Japan: correlation with porphyry copper systems. *Earth, Planets and Space*. 68(67): 1-11.
- Mitchell, J.K. and Soga, K. (2005). *Fundamentals of Soil Behavior*, 3rd Edition. United State of America: John Wiley and Sons, Inc.
- Ningrum, I.H., Irianto, H. and Riptanti, E.W. (2018). Analysis of soybean production and import trends and its import factors in Indonesia. Paper presented at the Earth and Environmental Science. Surakarta
- Orji, O.A. and Eke, I.P. (2018). Effect of mulch materials on soil physico-chemical properties and the performance of castor bean plant (*Ricinus communis*) in rivers state, Nigeria. *Indian Journal of Agricultural Research*. 52(6): 649-654.
- Ramos, C.G., de Mello, A.G. and Kautzmann, R.M. (2014). A preliminary study of acid volcanic rocks for stonemeal application. *Environmental Nanotechnology, Monitoring and Management*. 1-2: 30-35.
- Razaq, M., Zhang, P., Shen, H.L. and Salahuddin. (2017). Influence of nitrogen and phosphorous on the growth and root morphology of *Acer mono*. *PLoS One*. 12(2): e0171321.
- Roessali, W., Ekowati, T., Prasetyo, E. and Mukson, M. (2017). Supply response of the soybean in indonesia. Paper presented at the The 6th Indonesia Regional Science Associate (IRSA) International Institute: Maritime Infrastructure and Regional development in Manado. North Sulawesi.
- Singh, M., Jaswal, A. and Singh, A. (2019). Crop residue management for sustenance of natural resources and agriculture productivity. *Agricultural Reviews*. 40(3): 223-228.
- Suriadikusumah, A., Nugraha, W., Nurlaeny, N. and Devnita, R. (2013). Effect of different mixed media (merapi volcanic ash, cow manure and mineral soil) on chemical properties of soil and growth of maize (*Zea mays* L.). *Journal of Agricultural Science*. 5(2): DOI: 10.5539/jas.v5n2p188.
- Tan, K.H. (2011). *Principles of soil chemistry*. Boca Raton, FL.: CRC Press. Taylor and Francis Group.
- White, P.J. and Broadley, R.M. (2003). Calcium in Plants. *Ann Bot*. 92(4): 487-511.